PATTERNS OF DUCK COMMUNITY COMPOSITION IN THE PRAIRIE POTHOLE REGION OF CANADA: EFFECTS OF CLIMATE AND LAND USE

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By
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ABSTRACT

Shifts in the duck community composition in the Canadian Prairie Pothole Region (PPR) have been evident over the past 25 years for reasons that are not entirely clear. Several duck species have increased in abundance whereas others have remained stable, or have declined, despite shifts in agricultural land use from annually tilled cropland to more pasture and haylands, and increases in spring pond counts since 2008. I considered three main hypotheses that could account for species-specific changes in duck abundances within the Canadian PPR; (i) redistribution; (ii) climate and (iii) land use. First, I examined whether shifts in populations of eleven duck species (seven dabbling ducks, four diving ducks) could be due to redistribution from other regions either to or from the Canadian PPR. I found no support for this hypothesis for any species. Trends and timing of changes in duck abundances were generally similar and coincident in US prairie, Canadian PPR and southern boreal forest biomes in all species.

To test for effects of variations in climate, I used >20,000 nesting records for eight upland nesting duck species and related the timing of nesting and subsequent nest success to annual variations in spring temperature and moisture conditions. Furthermore, I tested for the relative importance of antecedent winter climate on nesting activities using winter El Niño Southern Oscillation indices. In general, nesting occurred earlier in warmer springs and following warmer, wetter winters. However, the magnitude of responses varied, indicating species-specific responses to variations in climate. Early nesting was the most influential factor for increasing nest survival and because timing advanced following wetter winters, this may provide a cross-seasonal mechanism for how winter climate can subsequently impact offspring recruitment in species like mallard (*Anas platyrhynchos*).

To evaluate the land use change hypothesis, I related changes in duck abundances to changes in ponds and upland habitat composition using unique monitoring data collected in the PPR in 1985 and 2011. I used data from 42 transects distributed across the PPR to first characterize changes in upland habitat and then relate these changes to abundances of four common dabbling duck species. Pond abundances increased between ~1985 and ~2011, and cropland was converted to tame grass (i.e., pastureland). Changes in abundances of mallard and northern shoveler (*A. clypeata*) were primarily driven by changes in pond abundances. In blue-winged teal (*A. discors*), abundances of breeding birds increased more rapidly than other species and there was some evidence that conversion of cropland to tame grass resulted in greater teal

abundances. Change in abundance of northern pintail (*A. acuta*) was not related to changes in ponds or upland habitat conditions.

Overall, I found no evidence for the redistribution hypothesis; however, I did find evidence for species-specific responses to both variations in climate and changes in land use. This implies that species respond differently to various drivers and may be a partial explanation for observed differences in population trajectories. Although further research should seek to explain increases in certain species over others, my work provides insights into potential species-specific population drivers. This information is critical in informing managers about possible areas where conservation actions could be implemented to sustain waterfowl populations.

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I would like to thank my committee: Drs. Jill Johnstone, Xulin Guo, and Kirsty Gurney, with a special thanks to Kirsty for always being available to answer questions and for statistical support. I was also very fortunate to have help from many collaborators: Drs. Jim Devries and Dave Howerter from Ducks Unlimited Canada Institute for Wetland and Waterfowl Research; Blake Bartzen, Mike Watmough, and Zhong Li from the Canadian Wildlife Service. The technical guidance and editorial support from these individuals really made this research possible. I would also like to thank >300 field personnel across various projects that helped in the collection of the datasets I was fortunate enough to have the opportunity to use for this research.

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I am thankful to the Aquatic Unit of the Canadian Wildlife Service for allowing me to take part in the Waterfowl Habitat and Breeding Population Survey. A special thanks to Keith Warner from this group for providing logistical support for my own field work. I am also thankful for the technical support and friendship of my fellow Clark lab mates and other Biology graduate students, namely Megan Ross. I am so grateful to have met such a great friend early on and that we were there to support each other at every step of this process.

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CHAPTER 1. INTRODUCTION

1.1 GENERAL BACKGROUND

The Canadian Prairie Pothole Region (PPR) is a large region spanning Alberta, Saskatchewan, and Manitoba (Figure 1.1), and is characterized primarily by pothole wetlands formed as a result of glacial depressions over thousands of years ago. These wetland basins vary in size and permanency class, from temporary and seasonal ponds to semi-permanent and permanent ponds, and provide varying habitat for diverse wetland-associated flora and fauna (Stewart and Kantrud 1971). The numbers and types of each wetland class vary with natural temperature (~10^{o}C increase from north to south) and precipitation (~600 mm/year increase from west to east) gradients and with the temporal wet and dry-cycles characteristic of this region (Millet et al. 2009). Because climate is a main driver of wetland conditions and land use practices in this landscape, it is important to consider how this region may change given recent climate change projections.

Global mean surface air temperature is expected to increase 0.3 to 0.7^{o}C with greatest warming in higher latitudes (Kirtman et al. 2013). Daily average temperatures in the PPR alone have already risen 1.0^{o}C over the long-term average since the late 19th century (Millet et al. 2009). Predictive modeling has suggested that a combined 3^{o}C increase in temperature and 10% decrease in precipitation will cause a 74% and 31% loss of the number of wetland basins in the Canadian parklands and grasslands, respectively (Larson 1995; Millet et al. 2009). Not only will increases in temperature affect the availability of wetland habitat for associated species, but the phenology of biological events may also advance. A 26-day advance in flowering date has already been documented in Alberta, Canada, indicating a shift in spring phenology which may have further impacts on other biological processes (Beaubien and Freeland 2000).

Changes in climate will not only directly affect the PPR landscape through mediating wetland conditions and timing of spring, but will also have indirect effects via changes in land use in response to changes in crop yields and prices. Historically, the PPR was mainly comprised of fescue, mixed, and tallgrass prairie; however, by 2001, about 55% of this region had been

cultivated. The most widespread crops are cereal (i.e., wheat or barley), canola, and legumes, such as peas and lentils. Although cultivation continues to dominate the landscape, tame grassland area increased since 1985 while amount of native grassland declined by 10% (Watmough and Schmoll 2007). With much of the landscape already altered by native habitat loss and fragmentation, predictive models suggests that further changes due to biofuel practices will decrease wetlands by 37-56% with especially high losses in Saskatchewan (Withey and van Kooten 2013). This will further exacerbate the landscape changes induced by changes in climate and have potentially detrimental effects on ecosystems within the region.

Although the PPR landscape has historically been subjected to variations in climate and altered via changes in land use practice, it is still the single most productive region for breeding waterfowl in North America (Batt et al. 1989). Because of the PPR's uncontested importance for breeding waterfowl, various management strategies and studies have been conducted to conserve and understand waterfowl production in this region. It is critical to understand the drivers of production and how various environmental and anthropogenic pressures impact breeding schedules and reproductive success of waterfowl species. During the past 25 years, duck community composition in the prairies has shifted from being dominated primarily by mallard (*Anas platyrhynchos*), northern pintail (*A. acuta*), and blue-winged teal (*A. discors*), to increased dominance of blue-winged teal, northern shoveler (*A. clypeata*), and gadwall (*A. strepera;* USFWS 2015). There is uncertainty about what may be driving these species-specific patterns.

1.2 THESIS OBJECTIVES AND ORGANIZATION

The primary objective of my research is to investigate species-specific variation in population trajectories that have resulted in a shift in the duck community composition in the PPR of Canada. My work considers multiple, non-exclusive hypotheses for observed trends in species-specific population abundances in the Canadian PPR. I have organized this thesis into three main data chapters, a synthesis, and an appendix. The data chapters were written as independent manuscripts for publication in peer-reviewed journals.

In Chapter 2, I use long-term population data for each species from the annual Waterfowl Breeding Population and Habitat Survey (USFWS & CWS 1987) to test for large scale redistributions of species over time within the Canadian PPR - either to or from the U.S. PPR and southern boreal forest. First, I test for negative correlations for each species' population between the three regions over time. Then, I test for asynchrony in population trends by using

residuals derived from a Gompertz density-dependence model to assess how populations between each region correlate with one another over a 40 year time series. Finally, I use models to test whether populations in the U.S. and Canadian PPR are uncoupled from pond counts.

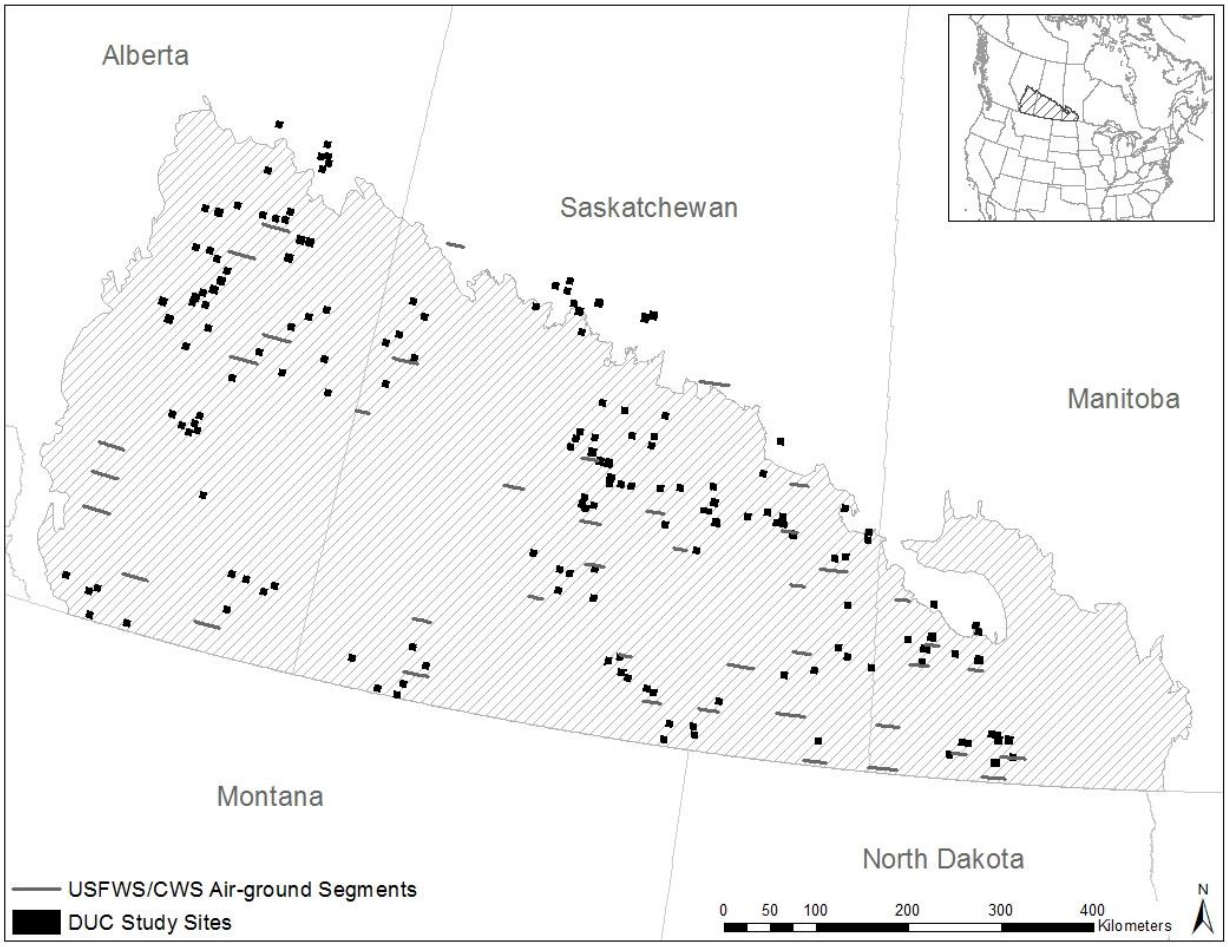
Because climate in the PPR is variable and changing, I assess the reproductive consequences of species-specific responses to variations in climate in Chapter 3. Many duck species have responded to climate change, arriving earlier on breeding grounds with increasing temperature (Murphy-Klassen et al. 2005) and earlier spring as a result of earlier ice thaw (Guillemain et al. 2013; Arzel et al. 2014). Along with advances in arrival date with increases in temperature, Drever and Clark (2007) showed that, in general, nest survival was positively related to temperature in five prairie-nesting duck species. Recently, Drever et al. (2012) suggested that warmer springs might benefit flexible species that could respond more quickly to changing phenology, whereas species with fixed breeding schedules would not. How antecedent and current climate conditions affect wetland abundances and processes will have important ramifications for duck populations and, hence, community composition (Sorenson et al. 1998). Therefore, in Chapter 3, I use duck nesting records from three multi-year studies conducted by Ducks Unlimited Canada (Figure 1.1) to assess how timing of nesting and subsequent nest survival are related to climate variables. I considered spring temperature as an index of spring phenology and winter El Niño Southern Oscillation index to represent possible cross-seasonal effects of over-winter climatic conditions on subsequent reproduction in several species of upland-nesting dabbling ducks.

In Chapter 4, I consider if changes in upland habitat can explain changes in duck abundance after accounting for changes in pond conditions. Duck abundance, for most species, tends to closely track the availability of ponds in the PPR (Krapu et al. 1983; Johnson and Shaffer 1987; Austin 2002; Sæther et al. 2008) and pond conditions have implications for nest success (Drever et al. 2007; Walker et al. 2013*b*; Howerter et al. 2014), brood occupancy (Walker et al. 2013*a*), and duckling survival (Bloom et al. 2012). Nesting ducks also respond to the composition of upland habitat that surrounds wetlands (e.g., Cowardin et al. 1985, Greenwood et al. 1995), due in part to species-specific habitat selection preferences. Because nest success generally increases in landscapes with higher proportions of grassland/herbaceous habitat (Stephens et al. 2005, Bloom et al. 2013, Howerter et al. 2014), and decreases in heavily cropped landscapes (Greenwood et al. 1995, Drever et al. 2007, Bloom et al. 2013) it is

important to consider how duck species respond to changes in upland habitat. For Chapter 4, I use upland habitat change and duck and pond abundance data from the Canadian Wildlife Service from 1985 to 2011 on 42 transects throughout the PPR (Figure 1.1). This data was used to test, on a species-specific basis, if changes in duck abundance over this period are related to changes in ponds and changes in upland habitat composition.

In Appendix A, I conducted a precursory analysis to that described in Chapter 3. Timing of nesting in waterfowl species has implications for reproductive success and eventual offspring recruitment (Blums et al. 2002), however, most descriptions to date are either qualitative or uncommon for certain species. Therefore, in Appendix A, I quantified the timing of nesting for nine upland-nesting duck species at 166 Canadian PPR sites over 34 years. I then related timing metrics to May pond counts as an index of habitat quality (Greenwood et al. 1995). In general, I found that May pond counts influenced the end of nesting date by extending the span of nesting for some species. This possibly reflects species-specific flexibility in (re-)nesting potential in response to favourable habitat conditions (Rotella et al. 2003; Arnold et al. 2010). Although I use pronoun "I" I would like to acknowledge the contributions of coauthors and reviewers. Appendix A was reprinted from: Raquel, A.J., J.H. Devries, D.W. Howerter, R.T. Alisauskas, S.W. Leach, and R.G. Clark. 2016. Timing of nesting of upland-nesting ducks in the Canadian prairies and its relation to spring wetland conditions. Canadian Journal of Zoology 94 (8):575-581, with permission from © Canadian Science Publishing or its licensors.

Figure 1.1 Map of the Canadian Prairie Pothole Region (hashed gray area) including Ducks Unlimited Canada study sites (1993-2011) used in Chapter 3 and Appendix A, and U.S. Fish and Wildlife Service/Canadian Wildlife Service Waterfowl Breeding Population and Habitat Survey air-ground comparison segments that correspond from 1985 to 2011 used in Chapter 4.



CHAPTER 2. CAN LARGE-SCALE REDISTRIBUTIONS OF BREEDING DUCKS EXPLAIN CHANGING PATTERNS IN DUCK COMMUNITY COMPOSITION IN THE CANADIAN PRAIRIES?

2.1 INTRODUCTION

Abundances of duck populations in the prairies are strongly related to the availability of ponds (Krapu et al. 1983; Johnson and Shaffer 1987; Austin 2002; Saether et al. 2008; Barker et al. 2014). However, many species are flexible and settle elsewhere when pond conditions on the prairies deteriorate (Johnson and Grier 1988). Specifically, in drought years in the prairies, many species shift their breeding distributions northward, presumably to take advantage of better pond conditions in northern regions (Smith 1970; Sorenson et al. 1998). This "over-flight" idea suggests that changes in distributions of species may be related to decreases in available habitat in one region coupled with increases in quality or quantity of habitat in another region, specifically that pond numbers in other areas may be more stable than those in the prairies (Johnson and Shaffer 1987). Therefore, movements of birds from the U.S. and Canadian prairies to other regions and biomes, especially in response to pond conditions, may explain observed temporal changes in the duck community composition (USFWS 2015).

2.1.1 Hypotheses and Predictions

The redistribution hypothesis proposes that changes in duck community composition across the Canadian Prairie Pothole Region (PPR) may be related to redistributions of breeding pairs over time to the U.S. PPR or southern boreal forest (SBF) or from these regions to the Canadian PPR (Figure 2.1).

If redistribution is occurring, annual population estimates will be negatively correlated and asynchronous among the three regions. I also evaluated how large-scale changes in duck abundances were related to region-specific pond counts. When considering population estimates between regions, the population in one region would be positively related with its region-specific pond counts whereas the population in the other region would be negatively related to its region-specific pond counts for redistribution to be occurring (Figure 2.2).

2.2 METHODS

2.2.1 Duck Population and Pond Count Data

Breeding duck population estimates and May pond counts at the stratum level were acquired from the U.S. Fish and Wildlife Service (USFWS)/Canadian Wildlife Service (CWS) Waterfowl Breeding Population and Habitat Survey (WBPHS) from 1974-2014 (USFWS and CWS 1987; https://migbirdapps.fws.gov/). Data were acquired for strata 26-40 (Canadian PPR), 41-49 (U.S. PPR), and 22, 25, 75 and 76 (SBF; see Figure 2.1) and then summed for each respective region to obtain regional population and pond estimates for each year (Figure 2.3). Reliable pond counts are not available for the SBF; therefore, this region was omitted from any analyses that considered relationships between population estimates and pond counts. All duck and pond abundance estimates were log transformed; however, due to zero values in the dataset a constant was added before transformation. Estimates were acquired for seven species of dabbling ducks: American wigeon (*Anas americana*; hereafter "wigeon"), blue-winged teal (*A. discors*), gadwall (*A. strepera*), American green-winged teal (*A. crecca carolinensis*), mallard (*A. platyrhynchos*), northern pintail (*A. acuta*; hereafter "pintail"), and northern shoveler (*A. clypeata*; hereafter "shoveler"); and four species of diving ducks: lesser scaup (*Aythya affinis*; hereafter "scaup"), canvasback (*Aythya valisineria*), redhead (*Aythya americana*), and ruddy duck (*Oxyura jamaicensis*).

2.2.2 Testing for Correlation and Asynchrony in Duck Abundance among Regions

All analyses were conducted in R 3.2.4 (R Core Team 2013). I calculated Pearson correlation coefficients of annual abundance estimates between U.S. PPR, Canadian PPR, and SBF from 1974-2014 to test for negative correlations between each species' population estimates in each region, separately. Furthermore, I calculated Pearson correlation coefficients of the residuals derived from a Gompertz density-dependence model to test for asynchrony between population estimates between each region over the same time period (Drever 2006).

2.2.3 Modelling Duck and Pond Abundance among Regions

I used general linear models to estimate population abundances in the U.S. and Canadian PPR considering effects of density-dependence, pond counts, and overall differences between regions. To test for redistribution, I included a region*pond interaction to test whether region-specific pond counts influenced population sizes such that opposing relationships with this

parameter between the two regions would suggest some evidence of redistribution. Models were run individually for each species. I used an information theoretic approach to model selection using Akaike's Information Criterion corrected for small sample size (AIC_c) and considered the most parsimonious model with only informative parameters to determine the best-approximating model given the data (Burnham and Anderson 2002; Arnold 2010).

2.3 RESULTS

2.3.1 Correlations in Duck Abundances among Regions

The only evidence of potential redistribution (i.e. negative correlation) was detected for blue-winged teal between the U.S. PPR and SBF (Table 2.1). Population estimates for wigeon, gadwall, green-winged teal, pintail, ruddy duck, and scaup were positively correlated between the SBF and Canadian PPR. Both teal species, canvasback, gadwall, mallard, pintail, and shoveler population estimates were positively correlated between the Canadian and U.S. PPR. Gadwall population estimates were positively correlated between the SBF and U.S. PPR.

2.3.2 Asynchrony in Duck Abundances among Regions

The only evidence of temporal asynchrony was detected in redhead population estimates between the U.S. and Canadian PPR (Table 2.2). Canvasback and pintail population estimates were synchronous between the U.S. PPR and SBF, and Canadian and U.S. PPR, respectively. None of the eleven species exhibited any detectable form of synchrony or asynchrony between the SBF and Canadian PPR.

2.3.3 Population Model – Duck and Pond Abundances

Models estimating population sizes of species between the U.S. and Canadian PPR provided limited evidence of redistribution. Mallard, blue-winged teal, and redhead were the only species that responded strongly to the interaction between pond count estimates and region (see Appendix B for model selection tables for each species). Parameter estimates were positive for all species (β=0.28 ± 0.11, β=0.27 ± 0.16, β=0.56 ± 0.21, respectively) as were the overall effects of pond counts (β=0.33 ± 0.08, β= 0.52 ± 0.12, β= 0.50 ± 0.15, respectively) indicating that both U.S. and Canadian populations of these species respond similarly to ponds. If one of these estimates was negative, that would indicate that the population of that region may be negatively related (i.e. uncoupled) to ponds and may be shifting, which is counter to the expectation that duck populations should be highly correlated with pond counts. There was some

evidence that the interaction between pond count estimates and region was important for canvasbacks, but this parameter was imprecisely estimated (β= 0.29 ± 0.18). Best-approximating models for all species included positive effects of the previous year's population estimate, positive effects of current year's pond counts, and an effect of region, with the exception of ruddy duck which exhibited no differences in population estimates between the U.S. and Canadian PPR. Pintail, gadwall, and shoveler were the only species with positive effects of region (β= 0.30 ± 0.12, β= 0.22 ± 0.08, β= 0.26 ± 0.09, respectively) indicating that the U.S. PPR population estimates were greater than those in the Canadian PPR.

2.4 DISCUSSION

Overall, I have found little support for the redistribution hypothesis. The only potential evidence of negative correlation was for blue-winged teal between U.S. PPR and SBF; however, only about 10% of the long-term total North American blue-winged teal population resides outside of the PPR (USFWS 2015) implying that population-level redistribution of this species to the SBF would a be substantial movement (i.e., easily detectable). The only evidence of asynchrony was between U.S. and Canadian PPR for redhead populations, but the best-approximating model for population estimates between these two regions included a positive effect of region-specific pond count. This suggests that populations within these regions may be asynchronous, but overall, each population is more influenced by ponds within that region such that populations are tracking pond counts, and not necessarily redistributing from one region to the other.

In the case of northern pintails, population estimates for the Canadian and U.S. PPR regions were positively related and synchronous. This means that over this time period population trends in both regions are similar and in each year, populations within each region are either increasing or decreasing at the same time. This implies that across the regions where pintails are most abundant (Johnson and Grier 1988), population fluctuations may be due to similar influences potentially acting at a broad scale.

Modelling population estimates of species between the U.S. and Canadian PPR resulted in no support for the redistribution hypothesis for any species, but it did reaffirm one obvious relationship: duck populations respond to pond counts (Krapu et al. 1983; Johnson and Shaffer 1987; Austin 2002; Sæther et al. 2008; Barker et al. 2014). Because of the limited and inconsistent evidence for redistribution, I conclude that changes in duck community composition

across the Canadian PPR are not likely related to redistributions of breeding pairs over time to or from the U.S. PPR or southern boreal forest. Therefore, other factors such as changes in climate and the ability of each species to respond to these changes, or changes in land use that favor certain species over others based on habitat affinities, may be valid alternative hypotheses to explore. I address these hypotheses in the next two chapters.

2.5 TABLES

Table 2.1 Pearson correlation coefficients of population estimates (log-scale) for duck species to test for negative correlations between the Canadian PPR, U.S. PPR, and southern boreal forest (SBF) over time (1974-2014). Bold values indicate strong effects (95% CI does not include 0).

Species†	Can PPR-SBF	Lower 95% CI	Upper 95% CI	US PPR-SBF	Lower 95% CI	Upper 95% CI	Can-US PPR	Lower 95% CI	Upper 95% CI
AGWT	**0.353**	**0.081**	**0.575**	0.106	-0.124	0.333	**0.504**	**0.290**	**0.693**
AMWI	**0.443**	**0.243**	**0.622**	0.194	-0.119	0.497	0.246	-0.061	0.532
BWTE	-0.246	-0.521	0.033	**-0.508**	**-0.692**	**-0.274**	**0.318**	**0.072**	**0.560**
CANV	-0.005	-0.324	0.281	0.172	-0.077	0.409	**0.374**	**0.127**	**0.595**
GADW	**0.301**	**0.014**	**0.568**	**0.484**	**0.231**	**0.691**	**0.545**	**0.381**	**0.740**
LESC	**0.554**	**0.337**	**0.719**	-0.226	-0.537	0.074	-0.186	-0.455	0.136
MALL	0.034	-0.280	0.334	0.019	-0.299	0.344	**0.343**	**0.016**	**0.651**
NOPI	**0.513**	**0.246**	**0.702**	-0.044	-0.356	0.278	**0.441**	**0.163**	**0.656**
NSHO	0.243	-0.064	0.550	0.159	-0.167	0.464	**0.573**	**0.394**	**0.721**
REDH	0.116	-0.183	0.402	-0.045	-0.291	0.192	0.263	-0.021	0.512
RUDU	**0.363**	**0.056**	**0.624**	0.142	-0.211	0.433	0.192	-0.104	0.435

† AGWT, American green-winged teal; AMWI, American wigeon; BWTE, blue-winged teal; CANV, canvasback; GADW, gadwall; LESC, lesser scaup; MALL, mallard; NOPI, northern pintail; NSHO, northern shoveler; REDH, redhead; RUDU, ruddy duck

Table 2.2 Pearson correlation coefficients of residuals derived from a Gompertz density-dependence model to test for temporal asynchrony in population size estimates for duck species in the Canadian PPR, U.S. PPR, and southern boreal forest (SBF) over time (1974-2014). Bold values indicate strong effects (95% CI does not include 0). Species acronyms are given in in Table 2.1.

Species	Can PPR-SBF	Lower 95% CI	Upper 95% CI	US PPR-SBF	Lower 95% CI	Upper 95% CI	Can-US PPR	Lower 95% CI	Upper 95% CI
AGWT	0.256	-0.065	0.570	0.038	-0.180	0.252	0.252	-0.130	0.541
AMWI	-0.097	-0.322	0.123	0.196	-0.108	0.456	-0.081	-0.351	0.223
BWTE	-0.128	-0.434	0.203	-0.145	-0.372	0.080	-0.134	-0.435	0.167
CANV	-0.200	-0.433	0.072	**0.274**	**0.023**	**0.492**	-0.044	-0.358	0.227
GADW	-0.095	-0.385	0.191	-0.096	-0.434	0.285	-0.174	-0.405	0.091
LESC	0.183	-0.121	0.441	0.223	-0.116	0.553	0.086	-0.149	0.303
MALL	-0.129	-0.479	0.270	0.014	-0.192	0.211	-0.077	-0.415	0.330
NOPI	0.199	-0.098	0.448	0.204	-0.076	0.463	**0.401**	**0.131**	**0.656**
NSHO	-0.285	-0.550	0.057	-0.186	-0.450	0.165	0.120	-0.148	0.375
REDH	0.116	-0.277	0.453	-0.142	-0.436	0.270	**-0.363**	**-0.589**	**-0.048**
RUDU	0.156	-0.140	0.428	-0.011	-0.469	0.382	0.051	-0.365	0.401

2.6 FIGURES

Figure 2.1 Map of the U.S. Fish and Wildlife Service and Canadian Wildlife Service Waterfowl Breeding Population and Habitat Survey (WBPHS) of the traditional survey strata for the Canadian Prairie Pothole Region (PPR; 26-40), U.S. Prairie Pothole Region (41-49), and Southern Boreal (22, 25, 75, 76).

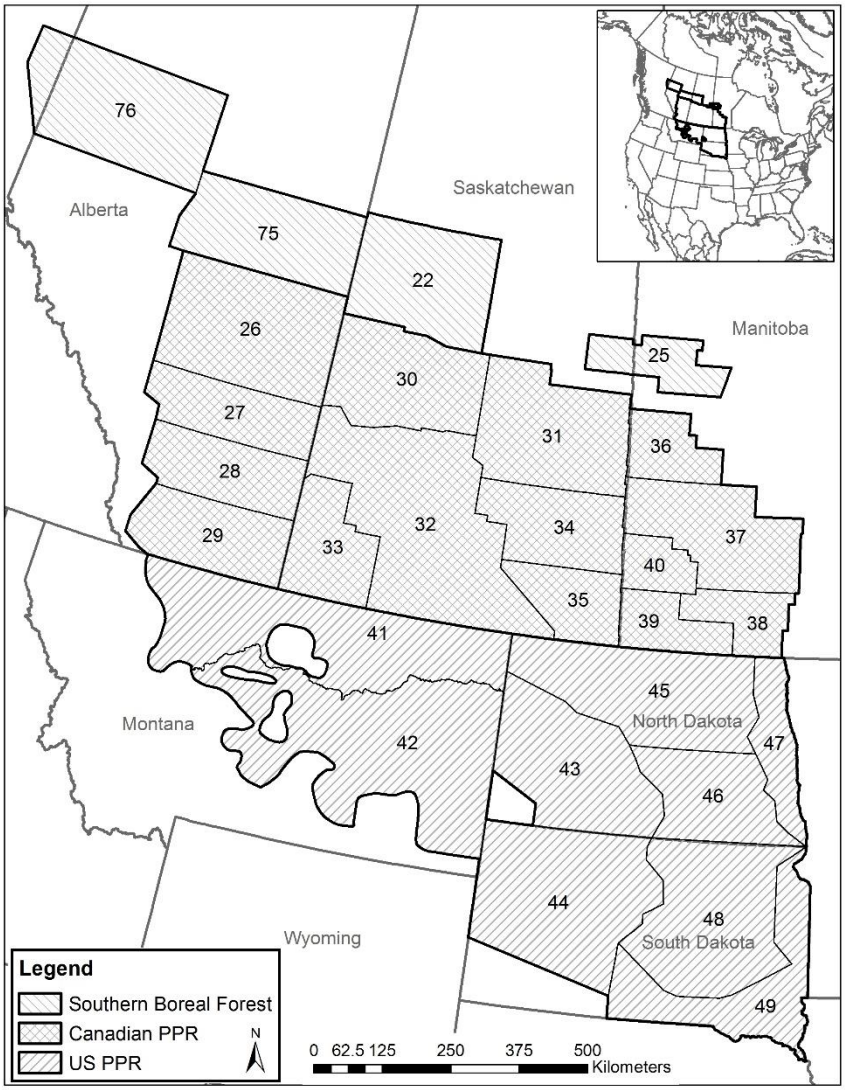


Figure 2.2 Possible patterns of pond counts (solid lines) relative to population estimates (dashed lines) between two regions (black vs. gray lines). Evidence for redistribution would result in population estimates in one region being positively correlated with pond counts in that region whereas population estimates in the other region would be negatively related to ponds counts in that region (Panel 1). If population estimates are positively related to pond counts in each respective region, then there is no evidence for redistribution (Panel 2).

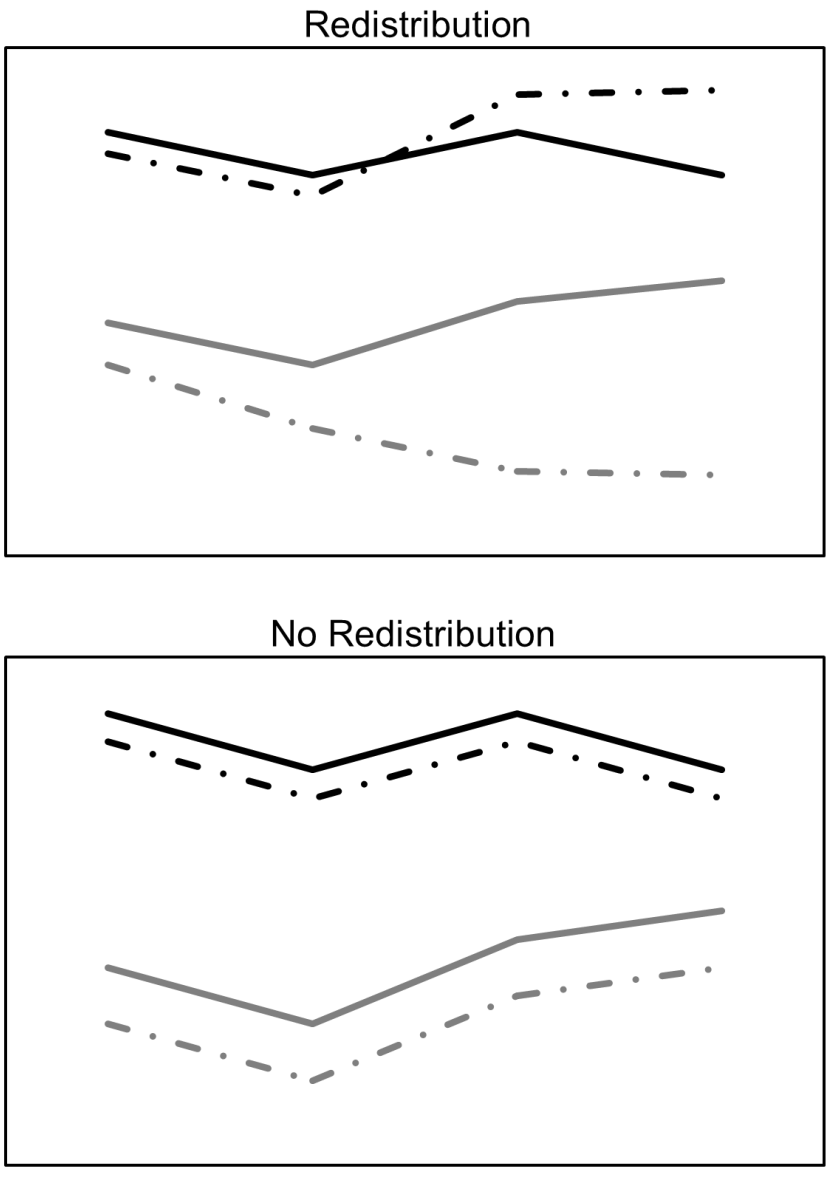
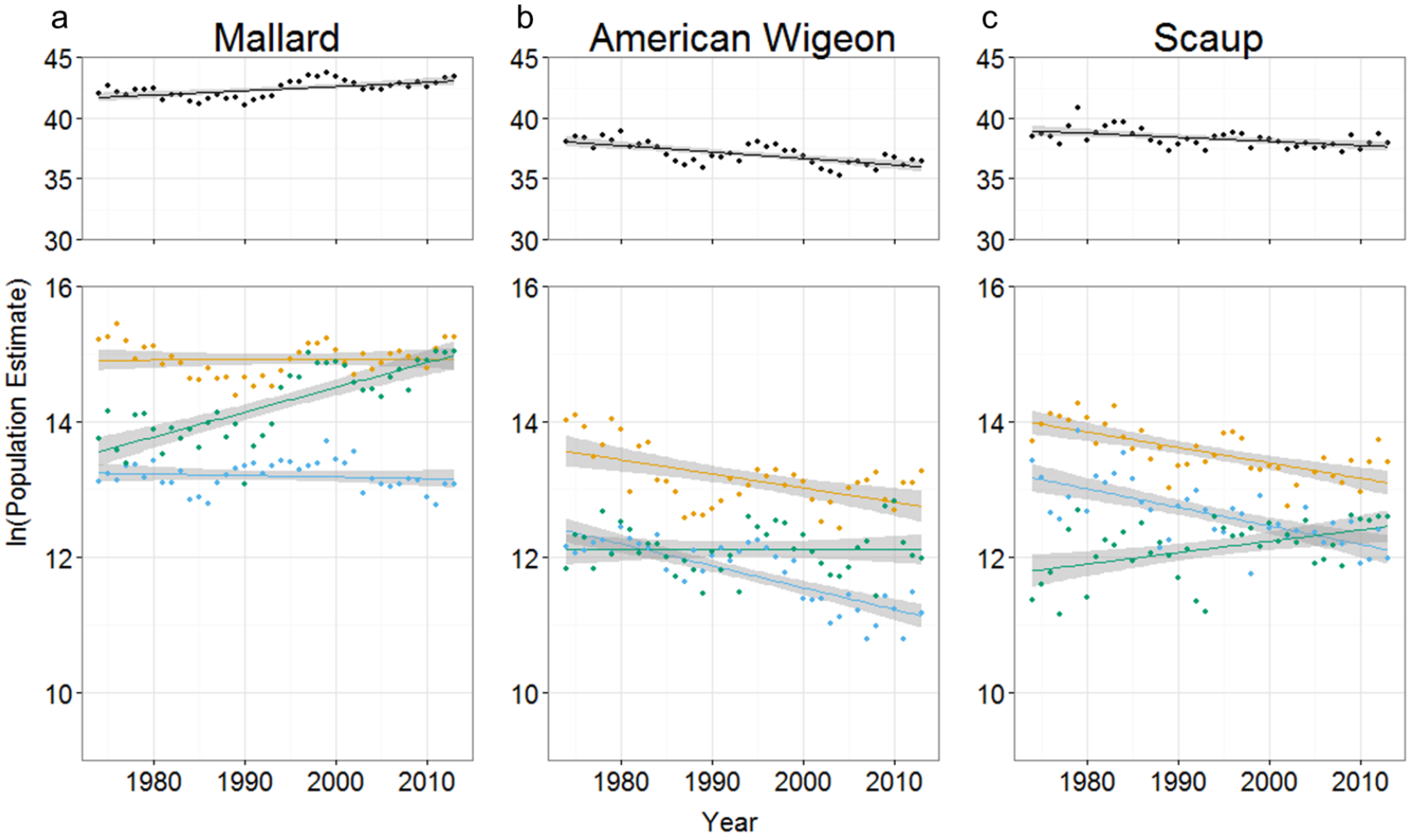
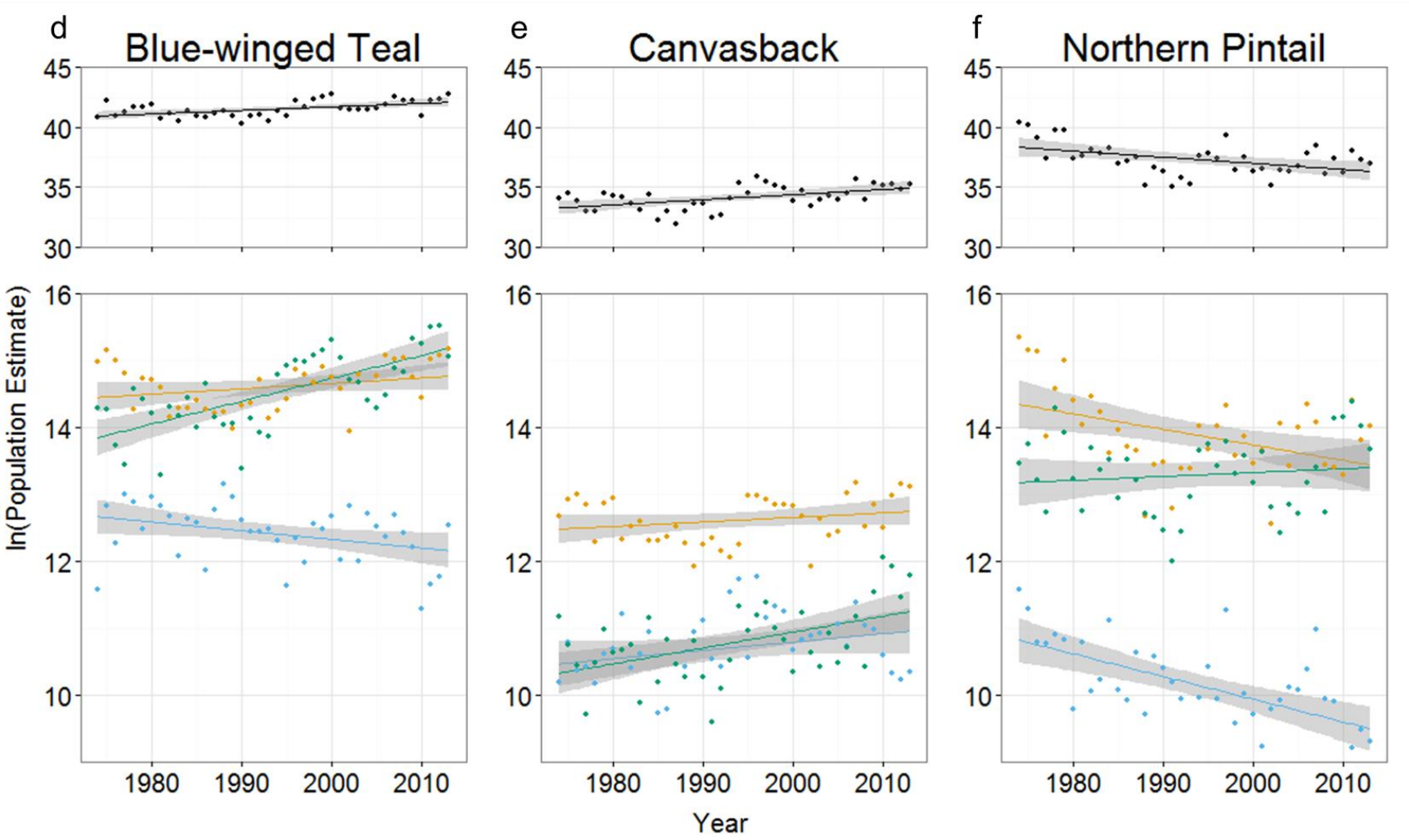
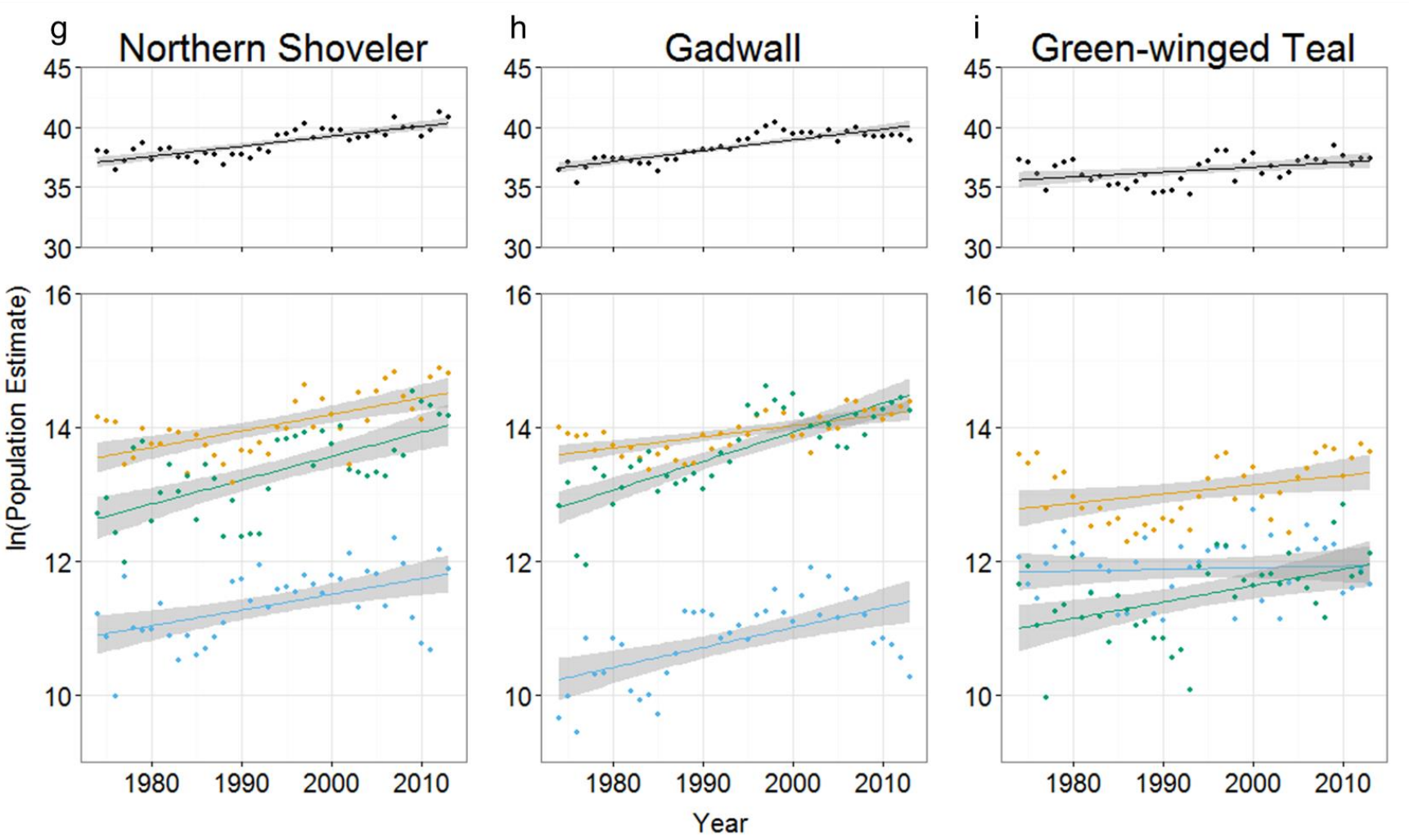


Figure 2.3 (Panels a-k). Population estimates (log-scaled) for the SBF (blue), Canadian PPR (orange), U.S. PPR (green), and combined total (black) for each of eleven species, 1974-2014, fitted with linear regression lines and 95% confidence intervals.




d
Blue-winged Teal
e
Canvasback
f
Northern Pintail
45
40
35
30
16
14
12
10
ln(Population Estimate)
1980
1990
2000
2010
Year


g
Northern Shoveler
h
Gadwall
i
Green-winged Teal
45
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ln(Population Estimate)
1980
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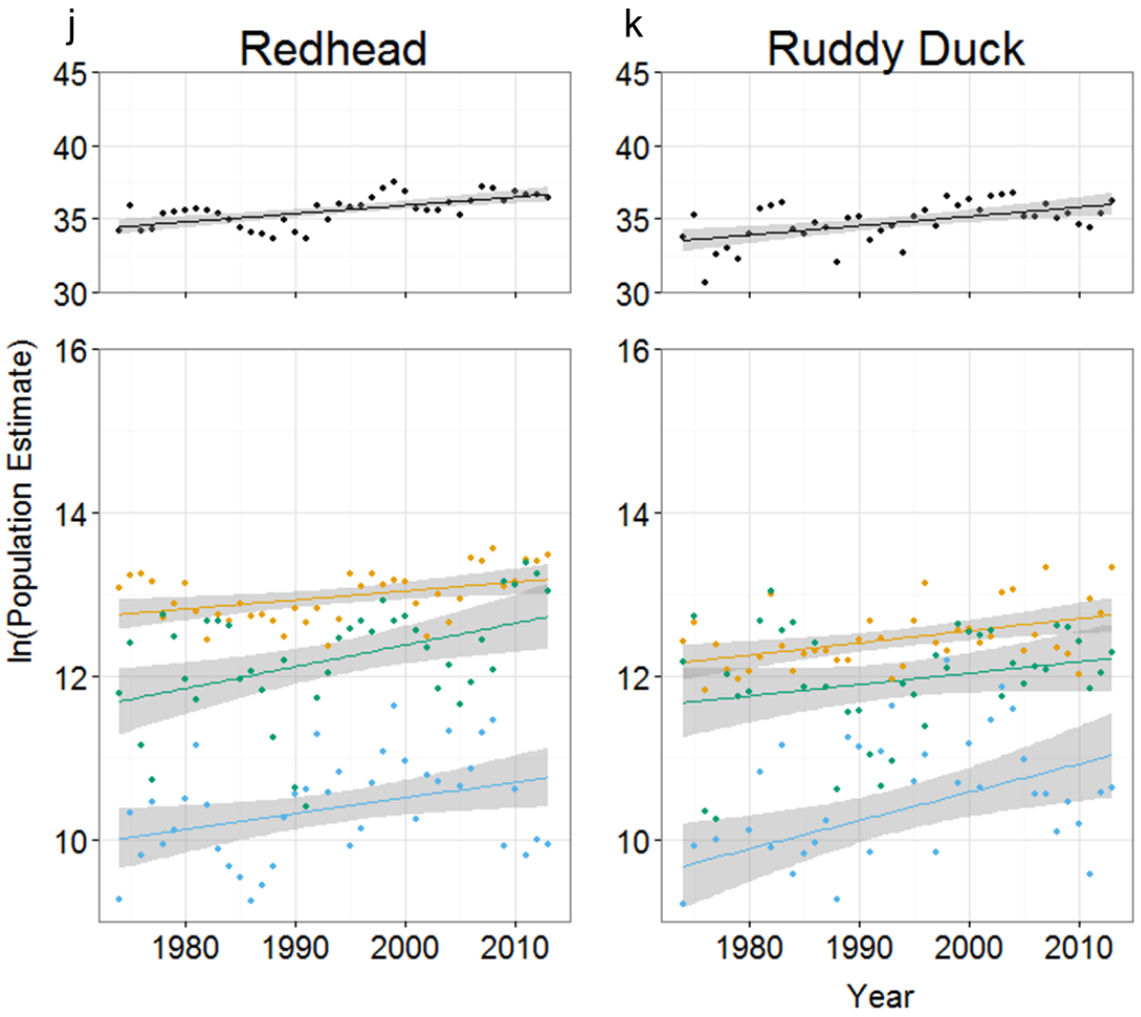
j
Redhead
k
Ruddy Duck
45
40
35
30
16
14
12
10
ln(Population Estimate)
1980
1990
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2010
Year

CHAPTER 3. REPRODUCTIVE CONSEQUENCES OF VARIATION IN CLIMATE: EVIDENCE FOR SPECIES-SPECIFIC RESPONSES TO SPRING PHENOLOGY AND CROSS-SEASONAL EFFECTS

3.1 INTRODUCTION

Climate change is rapidly becoming one of the most prominent forces impacting wildlife populations worldwide. With a projected increase of 0.3 to 0.7ºC in the global mean surface air temperature and an increase in precipitation in mid and high latitudes over the next two decades (Kirtman et al. 2013), plant and animal populations may be strongly affected, potentially leading to shifts in community structures. Alteration of current temperature and precipitation regimes could induce physiological effects, which may become more severe with further changes in the composition of the atmosphere. Additionally, changes in climate may affect distributions and ranges of species with local environmental changes, change species' phenologies as cues and as timing of co-dependent species change, and cause rapid adaptation and microevolution in species that regenerate quickly (Hughes 2000; Walther et al. 2002). Distributional and phenological shifts have already been documented for a suite of organisms, including plant species, butterflies, frogs, and birds (Parmesan and Yohe 2003).

Because migratory birds spend portions of their life-cycles in different locations, they often experience distinct climatic conditions at each locale. Conditions experienced during one stage of the life-cycle may then have impacts in subsequent life-cycle stages. These impacts are commonly referred to as carry-over effects if they act on individual fitness or cross-seasonal effects if they act on population dynamics; however, these are inextricably linked (Harrison et al. 2011; Sedinger and Alisauskas 2014). Specifically, conditions migratory birds experience during the winter may influence subsequent breeding success. Temperature and precipitation patterns, which influence primary productivity and in turn, food availability on the wintering grounds, can explain variation in body condition and departure dates (Marra et al. 1998), predict arrival dates to breeding grounds (Cotton 2003; Ahola et al. 2004; Gordo et al. 2005; Balbontín et al. 2009); and predict egg laying dates (McKellar et al. 2013). Birds experiencing dry winter conditions

occupy poorer quality (i.e. xeric) habitats which in turn can lower body condition (Paxton et al. 2014), delay arrival to breeding grounds (Rockwell et al. 2012; McKellar et al. 2013; Paxton and Moore 2015), delay nest initiation and reduce number of offspring fledged (Rockwell et al. 2012), and reduce clutch size and breeding success (Saino et al. 2004).

Global climate drivers, such as the El Niño Southern Oscillation index (ENSO), may also influence local climate conditions producing subsequent effects on species' activities during successive life-cycle stages. The ENSO is a global oceanic-atmospheric phenomenon that moderates annual variation of local climate conditions especially during December to March. ENSO conditions experienced overwinter may affect arrival date and body condition (González-Prieto and Hobson 2013) of birds, as well as survival and production of young (Sillett et al. 2000; Nott et al. 2002; Mazerolle et al. 2005). However, because the effects of ENSO vary geographically, impacts typically depend on species-specific distributions. For example, migratory birds wintering in Central America and the Caribbean have lower survival and fecundity following El Niño years (Sillett et al. 2000; Mazerolle et al. 2005). In contrast, Nott et al. (2002) showed that migratory songbirds wintering in Mexico had higher reproductive success following El Niño years. Although some evidence confirms the importance of these carry-over or cross-seasonal effects, some studies have shown that conditions experienced on the breeding grounds may be more important in predicting phenological shifts (Mazerolle et al. 2011; Ockendon et al. 2013).

Migratory birds can shift their migration and breeding phenologies to match local climatic conditions, but a species' ability to respond is likely related to its life history traits. Knudsen et al. (2011) and Møller et al. (2010) showed that several migratory bird species are arriving earlier on the breeding grounds as a result of climate change; for example, species with shorter migration distances, higher fecundity, simpler molting strategies, or more general habitat requirements (Végvári et al. 2010; Moussus et al. 2011). This may be partially due to the inability of long-distance migrants to reliably track and respond to environmental conditions during migration or on distant breeding areas (Both et al. 2009). Reproductive consequences may be more pronounced among species with limited flexibility in timing of breeding because of their limited ability to cope with environmental changes, including changing spring conditions (e.g., Gurney et al. 2011).

Warming spring temperatures have advanced the egg laying date of many species which can result in larger clutch sizes and increase the potential for re-nesting or producing multiple broods (Both and Visser 2001; Winkler et al. 2002). However, while advanced timing of reproduction may be advantageous for species with flexible breeding schedules, some authors have hypothesized that a detrimental mismatch could occur when the timing of reproduction and brood emergence become uncoupled from prey emergence. This uncoupling could lead to insufficient resources for young and, thereby, reduce reproductive success (e.g., Stenseth and Mysterud 2002; Knudsen et al. 2011). Species that are not able to adjust their phenology and respond to changes in the environment could suffer population declines (Møller et al. 2008).

Effective conservation and management of waterfowl populations requires consideration of conditions on wintering and breeding grounds, and how these conditions interact (reviewed in Sedinger and Alisauskas 2014). Several studies have simply evaluated whether the location where individuals or populations overwinter affects their timing of nesting and body condition on a common breeding ground (Mehl et al. 2004; Schamber et al. 2012; Gurney et al. 2014). Furthermore, studies have considered if the actual conditions experienced on these wintering grounds have carry-over or cross-seasonal effects on individuals and populations, respectively. For example, pink-footed geese (*Anser brachyrhynchus*) have lower body condition (Clausen et al. 2015) after experiencing harsher weather on the wintering grounds. Heitmeyer and Fredrickson (1981) and Kaminski and Gluesing (1987) further demonstrated that increased winter precipitation had a positive effect on subsequent recruitment of mallards. However, differences between these two studies in methodology, wetland indices, and sample sizes resulted in uncertainty between the relative importance of winter versus spring habitat conditions, nor were they able to specifically test putative mechanisms for higher productivity such as climatic effects on timing and of nesting, or nest success.

Similar to other migratory birds, waterfowl can respond to large-scale climatic drivers such as the North Atlantic Oscillation (NAO) or the ENSO index. Of these indices, most waterfowl studies to date have considered the effects of NAO and in European flyways. Here, NAO has been used as a metric for conditions on the wintering grounds and has resulted in earlier migrations following milder winters in several waterfowl species (Vähätalo et al. 2004; Lehikoinen et al. 2006; Rainio et al. 2006). However, no associations have been found between strength of winter NAO and timing of breeding (Oja and Pöysä 2007) or laying date (Lehikoinen

et al. 2006). Fewer waterfowl studies have considered the ENSO index and its importance in mediating climate patterns in North America. However, one such study has documented lower breeding probabilities in geese following El Niño years (Sedinger et al. 2006). Because these climatic drivers have a range of impacts on temperature and precipitation regimes over broad geographical scales, it is important to understand how these climate regimes impact individual species and determine their demographic consequences.

Ducks tend to arrive earlier on the breeding grounds during warmer spring weather conditions when snow and ice thaw earlier (Hammond and Johnson 1984; Murphy-Klassen et al. 2005; Guillemain et al. 2013; Arzel et al. 2014). Warmer springs also tend to advance nest initiation dates for species such as mallard (*Anas platyrhynchos*), northern pintail (*Anas acuta*; hereafter "pintail"), gadwall (*Anas strepera*), blue-winged teal (*Anas discors*), and redhead (*Aythya americana*; Langford and Driver 1979; Hammond and Johnson 1984). Additionally, Clark et al. (2014) showed that, in general, common goldeneye (*Bucephala clangula*) females adjusted their breeding phenology in response to spring lake-ice conditions. Further, Drever and Clark (2007) demonstrated that, in general, nest survival was positively related to temperature in five prairie-nesting duck species which may ultimately produce higher offspring recruitment. Because species have distinct flexibility in life history traits such as timing of nesting (Raquel et al. 2016), it is important to consider species-specific responses to understand how antecedent and current climate conditions affect reproductive success. Ultimately, this may have important ramifications for explaining species-specific differences in population trends and changes in duck community composition in the Canadian prairies (Sorenson et al. 1998).

3.1.1 Hypotheses and Predictions

I specifically wanted to test whether there are species-specific responses in timing of nesting to variations in spring conditions and wintering climate conditions based on the flexibility in breeding chronologies of each species. Furthermore, I wanted to examine if species-specific responses to variation in climate resulted in consequences for reproductive success. Therefore, my competing hypotheses are as follows: (1) females might only adjust in relation to spring conditions, as previously demonstrated (Langford and Driver 1979; Hammond and Johnson 1984; Drever and Clark 2007; Clark et al. 2014); (2) females may only adjust via cross-seasonal effects in relation to climate conditions on the wintering grounds (Mehl et al. 2004; Schamber et al. 2012; Gurney et al. 2014); (3) females may respond to both spring and winter

conditions, as suggested by previous work of Heitmeyer and Fredrickson (1981) and Kaminski and Gluesing (1987), however, the relative importance of spring vs. winter conditions is still uncertain; (4) the ability of females to respond could be related to their innate flexibility in breeding chronologies, such that "fixed" late-nesting species may have limited capacity to respond (Drever et al. 2012; Clark et al. 2014). My specific predictions are: (1) females of all species will nest earlier in warmer springs; (2) females of all species will nest earlier following warmer, wetter winters; (3) females of all species will nest earlier in warmer springs, especially those that are preceded by warmer, wetter winters; (4) females of "fixed", late-nesting species will show limited responses to climatic conditions compared to more "flexible" species in terms of the predictions of the previous three hypotheses. Furthermore, those species that exhibit greater capacity to respond to changes in climate either in spring and/or winter may have greater reproductive success.

3.2 METHODS

3.2.1 Study Area

I included sites from three duck nesting studies conducted by Ducks Unlimited Canada (PHJV Assessment Study, 1993–2000 [Howerter et al. 2014]; Pintail Study, 2005–2007; and Spatial/Temporal Variability Study [SpATS], 2002–2011). The Assessment study consisted of 27 65-km^2 sites, the Pintail study consisted of 17 41.4-km^2 study sites, and the SpATS study consisted of 120 41.4-km^2 study sites. I only include data for species and site-year combinations with ≥5 nests. All sites were located within the Canadian Prairie Pothole Region (PPR) which spans Alberta, Saskatchewan, and Manitoba and is characterized by flat to rolling terrain, dominated by agricultural cropland, and interspersed with numerous wetlands and remnant areas of grassland and woodland habitat.

3.2.2 Nest Searches

Nests were found by pulling a cable-chain between two all-terrain vehicles, hand-pulling ropes, or by beating vegetation with willow switches (Klett et al. 1986). Searches were conducted from early May through late June between 0730 and 1330 hr, each search at three week intervals, for a combination of three to four searches per site (Gloutney et al. 1993). When each nest (bowl with ≥1 egg) was found, date, species [wigeon, blue-winged teal, gadwall, American green-winged teal (*Anas crecca carolinensis*; hereafter "green-winged teal"), mallard,

pintail, northern shoveler (*Anas clypeata*; hereafter "shoveler"), and scaup], number of eggs, and incubation stage (Weller 1956) were recorded. Nest initiation dates were calculated by assuming a laying interval of 1 egg per day and that nest predation had not occurred unless evidence supported otherwise. Nests were visited every 6–10 days until nest fate could be determined. Nests were classified as successful if ≥1 egg hatched (Klett et al. 1986). Following each visit, observers covered eggs with nesting material to mimic normal female departures (Götmark 1992).

3.2.3 Climate Data

The Multivariate ENSO Index is derived from a principal component analysis consisting of six climatic components recorded in the Comprehensive Ocean-Atmosphere Data Set: sea level pressure, zonal and meridional wind components, sea surface and air temperatures, and total cloudiness. Negative values of this index are associated with La Niña events whereas positive values are associated with El Niño events (Wolter and Timlin 1993, 1998, 2011; https://climatedataguide.ucar.edu/). Winter El Niño events typically produce wetter conditions in the Texas Gulf Coast, California, and the Southern Plains of the United States (Wang et al. 1999). These regions are the main wintering and spring migration areas for most duck species studied, so I acquired ENSO data corresponding to the preceding wintering season (Dec–Feb) to be used as an index of climatic conditions experienced during winter.

Spring temperature was used as an index of spring phenology in the Canadian PPR. Onset of flowering, an index of timing of spring, is highly correlated with warmer temperatures (Rathcke and Lacey 1985), and flowering dates in Alberta, Canada, have advanced with increasing temperatures (e.g., Beaubien and Freeland 2000). Monthly temperature data were acquired from the CRU TS3.10 gridded climate dataset (Harris et al. 2014) for spring (Mar–Jun) for all study sites and then averaged across the four months at each site and across all sites in a single year to calculate a yearly average spring temperature index for the Canadian PPR.

The moisture anomaly index (Z-index) derived from the Palmer Drought Severity Index (Palmer 1965) was used to index spring moisture conditions. The Z-index is a measure of the monthly moisture anomaly from normal moisture conditions and is considered a valid measurement of drought in the Canadian PPR (Quiring and Papakryiakou 2003). Positive values are associated with wetter conditions whereas negative values are associated with drier conditions (Palmer 1965). Monthly moisture anomaly index values were acquired from the

National Agroclimate Information Service of Agriculture and Agri-Food Canada, averaged values across spring-summer months (Mar-Jun) for all sites, and then averaged across all sites in a single year to calculate a yearly average moisture anomaly index for the Canadian PPR. Index data were square-root transformed (1.04 added as a constant) to improve normality.

3.2.4 Timing of Nesting

To test how climatic factors might influence the start of nesting for each species while limiting re-nesting biases, 25% nesting dates were calculated for each species and site-year and I selected nest records initiated before this date (Raquel et al. 2016). General linear mixed effects models in program R version 3.2.4 (R Core Team 2013) were used to test whether antecedent winter conditions, spring temperature (biological null; Drever and Clark 2007), and spring moisture conditions influenced timing of nesting while accounting for random effects of site-year and habitat. I further considered species-specific responses by including interactions between a species term and each climatic variable. Because warmer temperatures (i.e. earlier springs) in the Canadian Prairies are associated with El Niño events (Beaubien and Freeland 2000), and because some collinearity was evident between Winter ENSO and Spring Temperature ($r = 0.31$, $p < 0.001$), I used the residuals of Spring Temperature (SPR_T_{resid}), derived from a general linear regression, in any model that incorporated both of these effects. I also considered an interaction between Winter ENSO and SPR_T_{resid} to examine if winter conditions mediated the effect of spring phenology on the timing of nesting of each species. Values of the interaction between Winter ENSO and SPR_T_{resid} were correlated with moisture anomaly indices, so these effects were never included in the same model. I also considered a statistical null model (intercept term only).

Because the preliminary analysis detected evidence of species-specific responses (i.e., species by climate index interactions), I then focused on how each species responded separately to climatic conditions. Using general linear mixed effects models, incorporating random effects of site-year and habitat, I tested for effects of Winter ENSO, moisture anomaly index (MAI), and the interaction between Winter ENSO, spring phenology (SPR_T_{resid} or SPR_T) on timing of nesting of each species. I also considered a statistical null model (intercept term only) and a biological null model that included effects of spring temperature (Drever and Clark 2007). Predicted values and 95% (unconditional) confidence intervals from the best-approximating model for each species were calculated using parametric bootstrap with 1000 replications.

Models in both analyses were part of a candidate set created to test predictions of specific hypotheses and were compared using Akaike's Information Criterion corrected for sample size (AIC_c; Burnham and Anderson 2002). The most appropriate random effects structure for each species-specific analysis was determined using likelihood ratio tests and retained all candidate models.

3.2.5 Nest Survival

To assess whether the ability of each species to respond to climatic conditions had subsequent effects on nest survival, I used generalized linear mixed effects models (GLMMs) in a logistic exposure analysis to model daily nest survival (accounting for the exposure period; Mayfield 1975) in relation to antecedent winter and current spring conditions while controlling for random effects of site-year (Rotella et al. 2004; Shaffer 2004; implemented in R by M. Herzog). Random effects structures were determined using likelihood ratio tests. Exploratory models, and previous studies (Klett et al. 1988; Greenwood et al. 1995; Emery et al. 2005) detected species-specific differences in nest survival, so each set of models was run individually for each species. Initially I tested for any effects of scaled relative initiation date (RCID; initiation date minus the 5% nest date for each species in each year; divided by maximum RCID for each species) and a quadratic effect of RCID against an intercept-only model (statistical null) to determine a biological null model for each species. Then more complex models were built that included effects of antecedent winter conditions (winter ENSO), spring phenology (SPR_T or SPR_T_{resid}, as above), and moisture anomaly index. Optimizers and number of iterations for models were adjusted to facilitate convergence. Models were compared using Akaike's Information Criterion adjusted for over-dispersion ($\hat{c}$ = residual deviance/df from the most parameterized model within the candidate set of models considered) and corrected for sample size ($QAIC_c$). Model selection uncertainty was reduced by selecting models with informative parameters (Burnham and Anderson 2002; Arnold 2010).

3.3 RESULTS

3.3.1 Timing of Nesting

Of the 21,230 nest records from 164 sites, the first 25% of nests for each species and site-year resulted in 5,838 nest records (Table 3.1 gives species-specific sample sizes). The best-approximating model included a species by winter ENSO interaction, species by SPR_T_{resid} interaction, a winter ENSO by SPR_T_{resid} interaction, and a three-way interaction between

species, winter ENSO and SPR_T_{resid} (Table 3.2). The overall effect of winter ENSO was negative indicating that, in general, nesting was earlier following El Niño years (i.e. wetter winters), but interactions indicate that species are responding differently to winter conditions. Additionally, the overall effect of relative spring temperature (SPR_T_{resid}) was negative signifying earlier nesting in warmer springs, but again strong interactions between species and SPR_T_{resid} indicate species-specific responses (Table 3.3).

Because of species-specific responses to climatic indices (i.e., significant interactions between species and climate indices), I further assessed how each species responded through individual species analyses. Although, I tested for effects of climate indices on the timing of nesting of all species, due to limited sample size, I focused my interpretations on the five most common species based on number of nests (n>1000; competitive models and parameter estimates ± SE are given in Table 3.4) but presented model selection tables and parameter estimates for wigeon, green-winged teal, and scaup in Appendix C.1. Each of the best-approximating models for four of the five most common species included negative effects of winter ENSO indicating that timing of nesting was earlier following warmer, wetter winters (Figure 3.1, Panel a). All of the five common species exhibited negative responses to relative spring temperature indicating that timing of nesting advances in warmer springs (Figure 3.1, Panel b), however, the magnitude of these responses varied by species. Equally competitive models for shoveler and pintail did not include effects of winter ENSO, but both species showed a weak positive response to moisture anomaly index by tending to nest later in years with wetter spring conditions (Figure 3.1, Panel c). The best-approximating models for mallard, blue-winged teal, and gadwall also included positive effects of the interaction between winter ENSO and relative spring temperature. This interaction manifested through more rapid advances in nesting date with increasing spring temperatures in La Niña years (negative values of ENSO) when compared with El Niño years (Figure 3.2, Panel a) or later nesting with increasing temperature in El Niño years, with the strongest response shown by mallard (Figure 3.2, Panel b).

3.3.2 Nest Survival

After removing research-related abandoned and manipulated nests, 19,391 nest records were included in the nest survival analyses (species-specific sample sizes in Table 3.1). Nest survival for blue-winged teal was most strongly influenced by a non-linear date effect; however, there is some evidence that climate indices may be important (Table 3.5). There is some

evidence suggesting moisture anomaly index had negative effects on nest survival indicating that wetter conditions were detrimental to nest survival. Nest survival for pintail was unaffected by any form of relative initiation date, with weak evidence of an effect of moisture anomaly index. Similar to blue-winged teal, wetter springs led to decreased nest survival for female pintails (Table 3.5).

Nest survival for gadwall was most strongly related to a non-linear date effect, with some indication that spring temperature may impact nest survival. An equally competitive model included a weak positive effect of spring temperature indicating that nest survival was higher during warmer springs. Mallard and shoveler showed similar patterns as gadwall, however, only a negative linear effect of date and no date effect, respectively, were important compared to the non-linear pattern exhibited by gadwall, but again nest survival for both mallard and shoveler females tended to increase during warmer springs.

Due to smaller sample sizes and greater convergence errors for American green-winged teal, wigeon, and scaup, I make limited inference of the effects of climate indices on nest survival, but present parameter estimates and model selection tables for comparison with future studies (Appendix C.2). Nest survival for these species tended to be most influenced by date effects with non-linear effects for wigeon, negative linear effects for scaup, and uncertainty between non-linear and linear effects for green-winged teal. There was also a weak positive effect of spring temperature on nest survival of wigeon.

3.4 DISCUSSION

Overall, my results highlight the importance of both spring temperature and winter conditions as drivers of nesting chronologies in several duck species based on the ability of each species to respond to varying climatic conditions. I was able to directly test the independent and interactive effects of winter and spring conditions on timing of nesting and determine if these have consequences for nest survival. Furthermore, my study provides new insights and evidence about mechanisms that may explain how favorable winter conditions result in greater reproductive success in some species and not others (e.g., Osnas et al. 2016).

3.4.1 Timing of Nesting

In general, my results are consistent with previous studies such that increases in temperature result in earlier nesting dates in most species (Langford and Driver 1979; Hammond and Johnson 1984). However, I also found evidence to support the flexibility hypothesis which

states that species with more plastic breeding chronologies may be more adept at responding to changes in spring climate. My results are consistent with those of Drever et al. (2012) such that mallard, as well as the additional common species I considered (shoveler, pintail, blue-winged teal, and gadwall), all seem to have flexible breeding schedules wherein females advance their nest initiation dates in response to earlier spring phenology, as indexed by increasing temperature. In contrast, but also consistent with the ideas of Drever et al. (2012), scaup appear to have a fixed breeding schedule and have limited response to changes in spring phenology; however, given smaller sample sizes compared with other species results or scaup should perhaps be viewed cautiously. Although female pintail did demonstrate the ability to alter nesting dates in response to changes in spring temperature, they also appeared to respond most strongly to the spring moisture anomaly index rather than winter conditions. Female pintails are among the earliest to nest, and whereas warmer temperatures (i.e. advances in spring phenology) may not create additional nesting opportunities, favorable moisture conditions may prolong the nesting season (Raquel et al. 2016).

I was also able to test the independent and interactive effects of winter and spring conditions on timing of nesting. In general, I found evidence that most common species, with the exception of pintail, tended to advance timing of nesting following El Niño winters, suggesting that when conditions are wetter on the wintering grounds (Wang et al. 1999) ducks may migrate north earlier or with better body condition, in turn triggering earlier arrival and nesting dates. My finding that pintail do not adjust timing of nesting in relation to winter conditions creates more uncertainty into mechanisms driving greater productivity following wintering ground precipitation for this species (Osnas et al. 2016). Better foraging conditions and reduced density-dependence may still result in better body condition for individual pintails which then may lay larger than average clutches, similar to other waterfowl species (Hamann and Cooke 1989; Lepage et al. 2000), resulting in the potential for production of more young. It may simply be that it is biologically impossible pintails to nest any earlier than they already do no matter if the conditions allow it, therefore, winter conditions must be acting on an alternate vital rate to increase productivity of this species, such as by increasing breeding propensity or renesting rate.

The ENSO index affects climate in different parts of the globe in different ways, the breeding grounds experience warmer, drier winters in El Niño years (Shabbar 2006) which typically result in earlier springs (Beaubien and Freeland 2000). Mallard, blue-winged teal, and

gadwall exhibited strong responses to the interaction of winter and spring conditions such that as spring temperature increased in El Niño years, nesting was later. This seems counter-intuitive, but the interaction between Winter ENSO and relative spring temperature is correlated with the moisture anomaly index (0.56, p <0.001), which suggests that winter conditions, along with spring temperature could set up favorable moisture conditions on the breeding grounds. Therefore, when spring ponds were abundant, these species had longer spans of nesting (Raquel et al. 2016) possibly due to an increase of (re)nesting later in the season or higher incidence of nesting by younger females. This possibly expanded the distribution of nest initiations for the season, shifting the 25% nest date later in response to later nesting attempts by female ducks in wetter springs.

Although most species exhibited some evidence of cross-seasonal effects on timing of nesting, the responses of different species do not seem to be consistent with the hypothesis that migration distance impacts the ability of a species to respond to variations in climate (reviewed by Knudsen et al. 2011). Long-distance migrants were as likely as short-distance migrants to adjust their migration and subsequent timing of nesting to changes in climate (Both et al. 2009). Blue-winged teal have the longest migrations, yet are one of the most responsive species in adjusting their timing of nesting in response to winter conditions. Wet winter conditions in the Gulf Coast area could extend farther south into Mexico and northern South America, where most blue-winged teal overwinter, or teal may encounter excellent wetland spring habitat conditions following wet winters in the Gulf Coast region, facilitating more rapid, early northward migration.

Because timing of nesting influences various reproductive rates including offspring recruitment in waterfowl populations (e.g., Dzus and Clark 1998; Dawson and Clark 2000; Blums et al. 2002) it begs the question as to why some species may demonstrate fixed breeding schedules and how this may be adaptive, especially for species such as scaup that seem to nest at a fixed time across widely-varying latitudes (Gurney et al. 2011). Scaup, as an example, need to forage selectively on invertebrates (relative to other species) to acquire sufficient protein for egg production (Baldassarre 2014). Therefore, female scaup may not track winter or breeding site conditions as closely because they are not ready to lay eggs when they arrive: onset of spring should not necessarily limit their breeding capability. They may, however, be more affected by local breeding site conditions that influence prey abundance. This late-nesting species may

rely more strongly on key amphipod prey that become available later in the season which may be important for egg production or duckling development (Dawson and Clark 1996), and nesting later may reduce competition for these resources. Another possible explanation may be that the quality of nesting cover improves as the season progresses which may further conceal nests and females from predators (Hines and Mitchell 1983). Or gadwall and scaup possibly associate more with semi-permanent and permanent ponds (Serie and Swanson 1976; Kantrud and Stewart 1977) as compared to the other species I studied which requires less reliance on environmental conditions that modify the quantity and quality of temporary and seasonal wetlands (Krapu 2000).

3.4.2 Nest Survival

Although most species capable of adjusting timing of nesting in response to variations in climate, direct effects of climatic variability on nest survival were rarely detected. Higher nest survival was observed in gadwall, mallard, and shoveler (to a lesser extent wigeon) during warmer springs which is consistent with findings of Drever and Clark (2007). Warmer springs may allow for higher nest attendance or more nesting opportunities for flexible species by extending time available for re-nesting. Another possibility is that vegetation grows faster in warming springs, providing greater nest concealment, especially from avian predators (Clark and Nudds 1991).

I also found weak evidence for detrimental effects of increased moisture conditions on nest survival for blue-winged teal and pintail. This may be a result of increased spring ponds extending the span of nesting (Raquel et al. 2016) due to an increase in later nesting attempts by younger or inexperienced females which typically have lower nest survival. Another possible explanation is that more females may nest in poorer habitat (agricultural areas) in wetter years which would result in overall lower nest success (e.g., Klett et al. 1988).

Date effects had the most consistent impact on nest survival across all species, with the exception of shoveler and pintail. Earlier nesting mallards, in particular, tended to have higher nest success which may provide a mechanism for how cross-seasonal effects influence recruitment (Heitmeyer and Fredrickson 1981; Kaminski and Gluesing 1987). Wetter winter conditions produced in El Niño years along the Gulf Coast and southern U.S. presumably provide more favorable habitat conditions and, in turn, greater foraging opportunities further dampening the effects of density-dependence (Osnas et al. 2016). This allows for greater

accumulation of endogenous reserves as ducks prepare for spring migration and reproduction (Heitmeyer and Fredrickson 1981; Heitmeyer 2006). Female mallards could migrate sooner, arrive earlier on breeding areas in better body condition and advance nesting dates (Devries et al. 2008). Because I demonstrated that winter ENSO resulted in earlier nesting for this species, and earlier nesting resulted in greater nest survival, this suggests that winter ENSO may have indirect effects on nest survival which may explain the documented higher recruitment of mallards following years with greater winter precipitation (Heitmeyer and Fredrickson 1981; Kaminski and Gluesing 1987).

Mallard, blue-winged teal, and gadwall all exhibited strong date effects on nest survival and strong effects of spring temperature on nesting date. This could imply that as temperatures continue to increase as projected by future climate scenarios (Kirtman et al 2013), these species will be able to advance nesting dates and subsequently have higher nest survival. Furthermore, because these species have the ability to advance nesting dates and earlier nesting is associated with higher reproductive success and recruitment (e.g., Dzus and Clark 1998; Dawson and Clark 2000; Blums et al. 2002), populations of these species would be expected to be sustained or potentially increase with increases in warmer conditions. Presumably, duck population growth would depend critically on how wetland conditions, food resources and predator respond to higher temperatures.

Collectively, my study provides evidence of reproductive consequences of species' responses to variations in climate for a suite of waterfowl species breeding in the Canadian prairies. Not only are these responses governed by breeding grounds conditions, but also by the climate regimes these birds experienced overwinter. This study provides new insights into drivers of species-specific abilities to alter nesting chronologies in response to climate variables and provides a mechanism for cross-seasonal effects on productivity of some species, but uncertainty remains for other species. Future work should consider the effects of more fine scale winter climate indices and conditions experienced during spring migration. This should be done at greater resolution (i.e. temperature and precipitation values from known areas) or at the individual level by tracking individuals and linking movement data visited to measures of subsequent survival and reproduction. Additionally, future studies should specifically test explanations for the fixed timing hypothesis which in turn may help explain the divergent population dynamics of late-nesting species (i.e. gadwall increasing, scaup numbers stable).

3.5 TABLES

Table 3.1 Number of nests and site-years included in the timing of nesting and nest survival analyses for each species. Timing of nesting analyses only considered nests initiated before the 25% date of each species and site-year whereas the nest survival analyses considered all nests except those abandoned or destroyed by research activities. The number of site years was the same for each species in each set of analyses.

	Timing	Nest Survival	
Species*	Nests	Nests	Site-years
AGWT	118	412	30
AMWI	107	360	24
BWTE	1924	6922	156
GADW	922	3206	109
LESC	107	345	25
MALL	1431	3770	130
NOPI	346	1236	67
NSHO	883	3140	120

* AGWT, American green-winged teal; AMWI, American wigeon; BWTE, blue-winged teal; GADW, gadwall; LESC, lesser scaup; MALL, mallard; NOPI, northern pintail; NSHO, northern shoveler

Table 3.2 Model selection table for timing of nesting related to Winter ENSO (WINT_ENSO), spring temperature (SPR_T; residuals, SPR_T_{resid}), and moisture anomaly index (MAI) from the overall analysis incorporating data for all species. Models that contain interactions also include the main effects of the variables within those interactions. Sample sizes (nests and site-years for each species) are given in Table 3.1.

Model Structure*	K[†]	Log likelihood	AIC_c[‡]	ΔAIC_c[§]	ω_i[‖]
SPECIES * WINT_ENSO + SPECIES * SPR_T_{resid} + WINT_ENSO * SPR_T_{resid} + SPECIES * WINT_ENSO * SPR_T_{resid}	35	-19163.98	38398.4	0	0.998
SPECIES * WINT_ENSO + SPECIES * SPR_T_{resid} + SPECIES * MAI	35	-19170.19	38410.8	12.42	0.002
SPECIES + WINT_ENSO + SPECIES * SPR_T_{resid} + SPECIES * MAI	28	-19194.38	38445.0	46.64	0
SPECIES * WINT_ENSO + SPECIES * SPR_T_{resid} + WINT_ENSO * SPR_T_{resid}	28	-19210.21	38476.7	78.29	0
SPECIES + WINT_ENSO + SPR_T_{resid} + SPECIES * MAI	21	-19218.31	38478.8	80.39	0
SPECIES * WINT_ENSO + SPECIES * SPR_T_{resid} + MAI	28	-19211.73	38479.7	81.35	0
SPECIES * WINT_ENSO + SPECIES * SPR_T_{resid}	27	-19216.06	38486.4	87.98	0
SPECIES * SPR_T_{resid} + WINT_ENSO * SPR_T_{resid}	21	-19231.14	38504.4	106.03	0
SPECIES + WINT_ENSO + SPECIES * SPR_T_{resid} + MAI	21	-19232.85	38507.9	109.46	0
SPECIES * WINT_ENSO + WINT_ENSO * SPR_T_{resid}	21	-19235.12	38512.4	114.00	0
SPECIES * WINT_ENSO + SPR_T_{resid} + MAI	21	-19236.58	38515.3	116.91	0
SPECIES * SPR_T (Biological null)	19	-19240.76	38519.6	121.24	0
SPECIES * MAI	19	-19247.91	38533.9	135.54	0
SPECIES + SPR_T_{resid} + WINT_ENSO * SPR_T_{resid}	14	-19256.99	38542.1	143.66	0
SPECIES + WINT_ENSO + SPR_T_{resid} + MAI	14	-19258.64	38545.3	146.94	0
SPECIES * SPR_T	12	-19263.94	38551.9	153.53	0
SPECIES * WINT_ENSO	19	-19260.85	38559.8	161.43	0
SPECIES + WINT_ENSO	12	-19282.82	38589.7	191.3	0
SPECIES + MAI	12	-19288.22	38600.5	202.08	0
SPECIES	11	-19289.37	38600.8	202.38	0
Intercept-only (Statistical null)	4	-22641.45	45290.9	6892.5	0

* The same site-year and habitat random effects structure was used in all models.

† Number of parameters included in the model.

‡ Akaike's Information Criterion corrected for small sample size (AIC_c).

§ Difference in AIC_c (ΔAIC_c) values between each model and the model with the lowest AIC_c are given.

‖ The Akaike weight (ω_i) or likelihood of a model, given the set of models.

Table 3.3 Parameter estimates ± SE from the best-approximating mixed effects model relating timing of nesting of species to Winter ENSO (WINT_ENSO), relative spring temperature (residuals, SPR_T_{resid}), and the interaction between Winter ENSO and relative spring temperature. MALL represents the reference intercept. Model structure is given in Table 3.2. Species acronyms are given in Table 3.1.

	Parameter Estimates ± SE			
	Species	WINT_ENSO	SPR_T_{resid}	WINT_ENSO * SPR_T_{resid}
Intercept (MALL)	123.39 ± 0.81	-2.28 ± 0.51[†]	-1.03 ± 0.45[†]	3.93 ± 0.74[a]
AGWT	13.13 ± 0.69	1.64 ± 0.57	0.01 ± 0.70	-0.70 ± 1.07
AMWI	21.66 ± 0.68	-0.12 ± 0.57	-2.40 ± 0.79	-3.69 ± 1.19
BWTE	15.77 ± 0.24	0.43 ± 0.18	-1.72 ± 0.23	-1.24 ± 0.35
GADW	26.16 ± 0.28	-0.26 ± 0.22	-1.40 ± 0.27	-1.60 ± 0.40
LESC	34.48 ± 0.69	1.81 ± 0.58	0.36 ± 0.75	-0.41 ± 1.07
NOPI	-3.19 ± 0.44	1.42 ± 0.42	-0.86 ± 0.42	-3.18 ± 0.64
NSHO	11.43 ± 0.29	0.65 ± 0.24	-1.76 ± 0.27	-3.36 ± 0.40

[†] The first β is the main effect of each variable, corresponding with mallard; the other βs in the column refer to interaction effects between species and each climate variable.

Table 3.4 Model selection tables including parameter estimates ± SE for competitive models (ΔAIC_c <4) for **timing of nesting** related to moisture anomaly index (MAI), Winter ENSO (WINT_ENSO), and spring temperature (SPR_T; residuals, SPR_T_{resid}) for each of the five most common species. Models that contain interactions also include the main effects of the variables within those interactions. Sample sizes (nests and site-years) for each species are given in Table 3.1.

	Parameter Estimates ± SE								
Model Structure*	MAI	WINT_ENSO	SPR_T/SPR_Tresid	WINT_ENSO * SPR_Tresid	K[†]	Log likelihood	AIC_c[‡]	ΔAIC_c[§]	ω_i[‖]
Blue-winged Teal									
WINT_ENSO + SPR_T_resid + WINT_ENSO * SPR_Tresid		-1.97 ± 0.55	-2.03 ± 0.45	3.10 ± 0.75	7	-5887.53	11789.1	0	0.88
Gadwall									
WINT_ENSO + SPR_T_resid + WINT_ENSO * SPR_Tresid		-1.88 ± 0.50	-2.51 ± 0.42	2.03 ± 0.70	7	-2803.01	5620.1	0	0.48
MAI + WINT_ENSO + SPR_Tresid	3.23 ± 1.25	-1.91 ± 0.51	-3.10 ± 0.43		7	-2803.30	5620.7	0.57	0.36
MAI + SPR_T	3.02 ± 1.26		-3.34 ± 0.42		6	-2805.26	5622.6	2.47	0.14
Mallard									
WINT_ENSO + SPR_T_resid + WINT_ENSO * SPR_Tresid		-2.12 ± 1.02	-1.81 ± 0.86	4.94 ± 1.45	7	-4674.27	9362.6	0	0.98
Northern pintail									
MAI + WINT_ENSO + SPR_Tresid	6.11 ± 2.34	-0.13 ± 1.00	-1.76 ± 1.07		7	-1156.05	2326.4	0	0.38
MAI + SPR_T	6.08 ± 2.33		-1.60 ± 0.96		6	-1157.12	2326.5	0.06	0.36
MAI	5.48 ± 2.32				5	-1159.37	2328.9	2.48	0.11
MAI + WINT_ENSO	5.51 ± 2.34	-0.35 ± 1.00			6	-1158.39	2329.0	2.59	0.1
Northern shoveler									
MAI + WINT_ENSO + SPR_Tresid	3.12 ± 1.80	-1.69 ± 0.76	-2.74 ± 0.64		7	-2883.23	5780.6	0	0.44
MAI + SPR_T	2.87 ± 1.78		-2.96 ± 0.61		6	-2884.51	5781.1	0.55	0.34
WINT_ENSO + SPR_T_resid + WINT_ENSO * SPR_Tresid		-1.57 ± 0.76	-2.27 ± 0.63	1.14 ± 1.00	7	-2884.66	5783.5	2.88	0.11
WINT_ENSO + SPR_Tresid		-1.42 ± 0.74	-2.41 ± 0.61		6	-2886.23	5784.6	3.98	0.06

* The same site-year and habitat random effects structure was used in all models.

† Number of parameters included in the model.

‡ Akaike's Information Criterion corrected for small sample size (AIC_c).

§ Difference in AIC_c (ΔAIC_c) values between each model and the model with the lowest AIC_c are given.

‖ The Akaike weight (ω_i) or likelihood of a model, given the set of models.

Table 3.5 Model selection tables including parameter estimates ± SE for all models for **daily nest survival** related to relative initiation date (RCID) and the quadratic form ($RCID^2$), moisture anomaly index (MAI), Winter ENSO (WINT_ENSO), and spring temperature (SPR_T; residuals, SPR_T_{resid}) for each of the five most common species. Over-dispersion parameter (ĉ) calculated from the most parameterized model within the candidate set of models considered is given for each species. Models below the dashed line for any given species did not converge. Sample sizes (nests and site-years) for each species are given in Table 3.1.

	Parameter Estimates ± SE								
Model Structure*	RCID	$RCID^2$	MAI	WINT_ENSO	SPR_T/SPR_T_{resid}	K[†]	$QAIC_c$[‡]	$\Delta QAIC_c$[§]	ω_i[‖]
Blue-winged teal **(ĉ=2.04)**									
RCID + $RCID^2$	0.801 ± 0.269	-1.183 ± 0.333				4	7108.3	0.00	0.28
RCID + $RCID^2$ + MAI	0.796 ± 0.269	-1.172 ± 0.333	-0.226 ± 0.137			5	7109.0	0.68	0.20
RCID + $RCID^2$ + WINT_ENSO	0.802 ± 0.269	-1.184 ± 0.333		0.008 ± 0.062		5	7110.3	1.99	0.10
RCID + $RCID^2$ + SPR_T	0.800 ± 0.269	-1.181 ± 0.333			-0.006 ± 0.048	5	7110.3	2.00	0.10
RCID + $RCID^2$ + WINT_ENSO + MAI	0.799 ± 0.269	-1.176 ± 0.333	-0.241 ± 0.140	0.031 ± 0.063		6	7110.8	2.57	0.08
RCID + $RCID^2$ + SPR_T + MAI	0.800 ± 0.269	-1.178 ± 0.333	-0.244 ± 0.144		0.020 ± 0.050	6	7110.9	2.61	0.08
intercept only						2	7111.3	3.02	0.06
RCID + $RCID^2$ + WINT_ENSO + SPR_T_{resid}	0.800 ± 0.269	-1.182 ± 0.333		0.009 ± 0.062	-0.009 ± 0.051	6	7112.3	3.98	0.04
RCID	-0.111 ± 0.080					3	7112.4	4.09	0.04
RCID + $RCID^2$ + WINT_ENSO + SPR_T_{resid} + MAI	0.801 ± 0.269	-1.180 ± 0.333	-0.251 ± 0.145	0.030 ± 0.063	0.014 ± 0.052	7	7112.8	4.54	0.03
Gadwall **(ĉ=2.07)**									
RCID + $RCID^2$	0.580 ± 0.488	-2.061 ± 0.708				4	3326.4	0.00	0.24
RCID + $RCID^2$ + SPR_T	0.585 ± 0.488	-2.083 ± 0.709			0.118 ± 0.060	5	3326.5	0.11	0.23
RCID + $RCID^2$ + WINT_ENSO	0.582 ± 0.488	-2.070 ± 0.708		0.060 ± 0.076		5	3328.1	1.70	0.10
RCID + $RCID^2$ + MAI	0.579 ± 0.488	-2.061 ± 0.708	0.060 ± 0.182			5	3328.4	1.95	0.09
RCID	-0.776 ± 0.148					3	3328.4	2.03	0.09
RCID + $RCID^2$ + SPR_T + MAI	0.587 ± 0.488	-2.085 ± 0.708	-0.064 ± 0.189		0.125 ± 0.063	6	3328.5	2.07	0.09
RCID + $RCID^2$ + WINT_ENSO + SPR_T_{resid}	0.586 ± 0.488	-2.084 ± 0.708		0.043 ± 0.076	0.116 ± 0.064	6	3328.5	2.12	0.09
RCID + $RCID^2$ + WINT_ENSO + MAI	0.581 ± 0.488	-2.070 ± 0.709	0.033 ± 0.185	0.058 ± 0.078		6	3330.1	3.70	0.04

RCID + $RCID^2$ + WINT_ENSO + SPR_T_{resid} + MAI	0.588 ± 0.488	-2.086 ± 0.708	-0.067 ± 0.190	0.047 ± 0.077	0.122 ± 0.066	7	3330.5	4.07	0.03
intercept only						2	3339.5	13.10	0.00
Mallard **(ĉ=2.08)**									
RCID	-0.571 ± 0.105					3	3919.8	0.00	0.25
RCID + SPR_T	-0.575 ± 0.105				0.118 ± 0.067	4	3920.4	0.54	0.19
RCID + $RCID^2$	-0.176 ± 0.358	-0.508 ± 0.440				4	3921.2	1.37	0.13
RCID + WINT_ENSO	-0.574 ± 0.105			0.077 ± 0.085		4	3921.4	1.62	0.11
RCID + MAI	-0.572 ± 0.105		0.065 ± 0.193			4	3921.8	1.95	0.10
RCID+ SPR_T + MAI	-0.575 ± 0.105		-0.061 ± 0.204		0.125 ± 0.072	5	3922.3	2.51	0.07
RCID + WINT_ENSO + SPR_T_{resid}	-0.576 ± 0.105			0.059 ± 0.085	0.110 ± 0.072	5	3922.3	2.51	0.07
RCID + WINT_ENSO +MAI	-0.574 ± 0.105		0.031 ± 0.197	0.074 ± 0.087		5	3923.4	3.61	0.04
RCID + WINT_ENSO + SPR_T_{resid} + MAI	-0.576 ± 0.105		-0.067 ± 0.205	0.063 ± 0.087	0.118 ± 0.076	6	3924.3	4.47	0.03
intercept only						2	3931.9	12.06	0.00
Northern pintail **(ĉ=1.98)**									
intercept only						2	1300.3	0.00	0.25
MAI			-0.363 ± 0.205			3	1300.7	0.47	0.20
WINT_ENSO				-0.112 ± 0.089		3	1301.5	1.22	0.14
WINT_ENSO + MAI			-0.362 ± 0.202	-0.111 ± 0.086		4	1301.9	1.65	0.11
RCID	0.109 ± 0.177					3	1302.1	1.82	0.10
SPR_T + MAI			-0.342 ± 0.205		-0.065 ± 0.085	4	1302.5	2.20	0.08
WINT_ENSO + SPR_T_{resid}				-0.107 ± 0.089	-0.047 ± 0.094	4	1303.4	3.11	0.05
RCID + $RCID^2$	0.477 ± 0.585	-0.446 ± 0.677				4	1303.9	3.62	0.04
WINT_ENSO + SPR_T_{resid} + MAI			-0.354 ± 0.203	-0.109 ± 0.087	-0.025 ± 0.093	5	1303.9	3.64	0.04
SPR_T									
Northern shoveler **(ĉ=2.01)**									
SPR_T					0.149 ± 0.061	3	3271.7	0.00	0.22
WINT_ENSO + SPR_T_{resid}				-0.066 ± 0.075	0.185 ± 0.065	4	3272.6	0.89	0.14
intercept only						2	3272.6	0.89	0.14

RCID	-0.235 ± 0.120					3	3272.7	1.00	0.13
SPR_T +MAI			-0.252 ± 0.190		0.179 ± 0.065	4	3272.8	1.15	0.12
WINT_ENSO + SPR_T_{resid} + MAI			-0.214 ± 0.190	-0.046 ± 0.077	0.206 ± 0.068	5	3274.0	2.28	0.07
WINT_ENSO				-0.036 ± 0.077		3	3274.5	2.79	0.05
MAI			-0.068 ± 0.182			3	3274.5	2.84	0.05
RCID + $RCID^2$	-0.295 ± 0.388	0.079 ± 0.487				4	3274.7	2.99	0.05
WINT_ENSO + MAI			-0.049 ± 0.188	-0.031 ± 0.079		4	3276.5	4.77	0.02

[*] The same site-year random effects structure was used in all models.

[†] Number of parameters included in the model.

[‡] Akaike's Information Criterion corrected for sample size and over-dispersion ($QAIC_c$).

[§] Difference in $QAIC_c$ ($\Delta QAIC_c$) values between each model and the model with the lowest $QAIC_c$ are given.

[‖] The Akaike weight (ω_i) or likelihood of a model, given the set of model.

3.6 FIGURES

Figure 3.1 Timing of nesting (± unconditional 95% CI; days since 1 January) estimated the best-approximating mixed effects model for each species separately in relation to a) winter ENSO, b) relative spring temperature (SPR_T_{resid}), and c) moisture anomaly index (MAI) for each of the five most common dabbling duck species (long dash as gadwall, dot dash as blue-winged teal, dotted as shoveler, solid as mallard, dash as pintail). All other variables were held constant when not under consideration, SPR_T_{resid} held at mean of ~0, Winter ENSO held at mean of~0, MAI held at mean of ~1. Positive (negative) values of relative spring temperature are associated with warmer, earlier (cooler, later) springs on the breeding grounds. Positive (negative) values of Winter ENSO are associated with wetter, cooler (warmer, drier) conditions on the wintering grounds. Larger values of MAI represent wetter spring conditions. Parameter estimates ± SE for all species are given in Table 3.4.

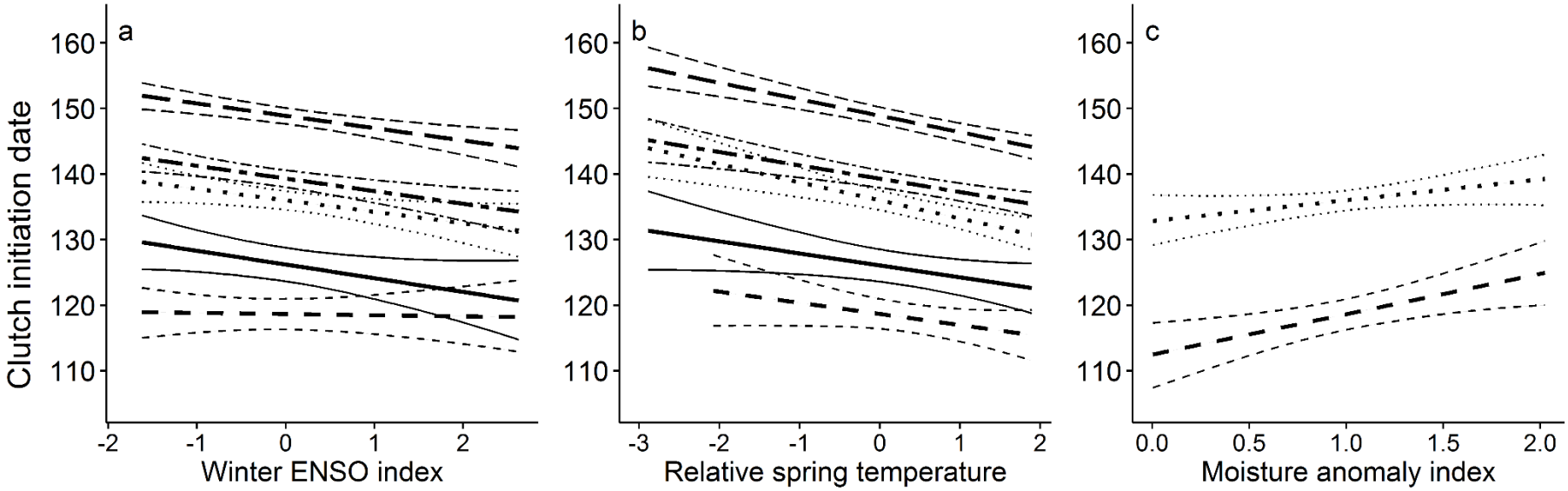
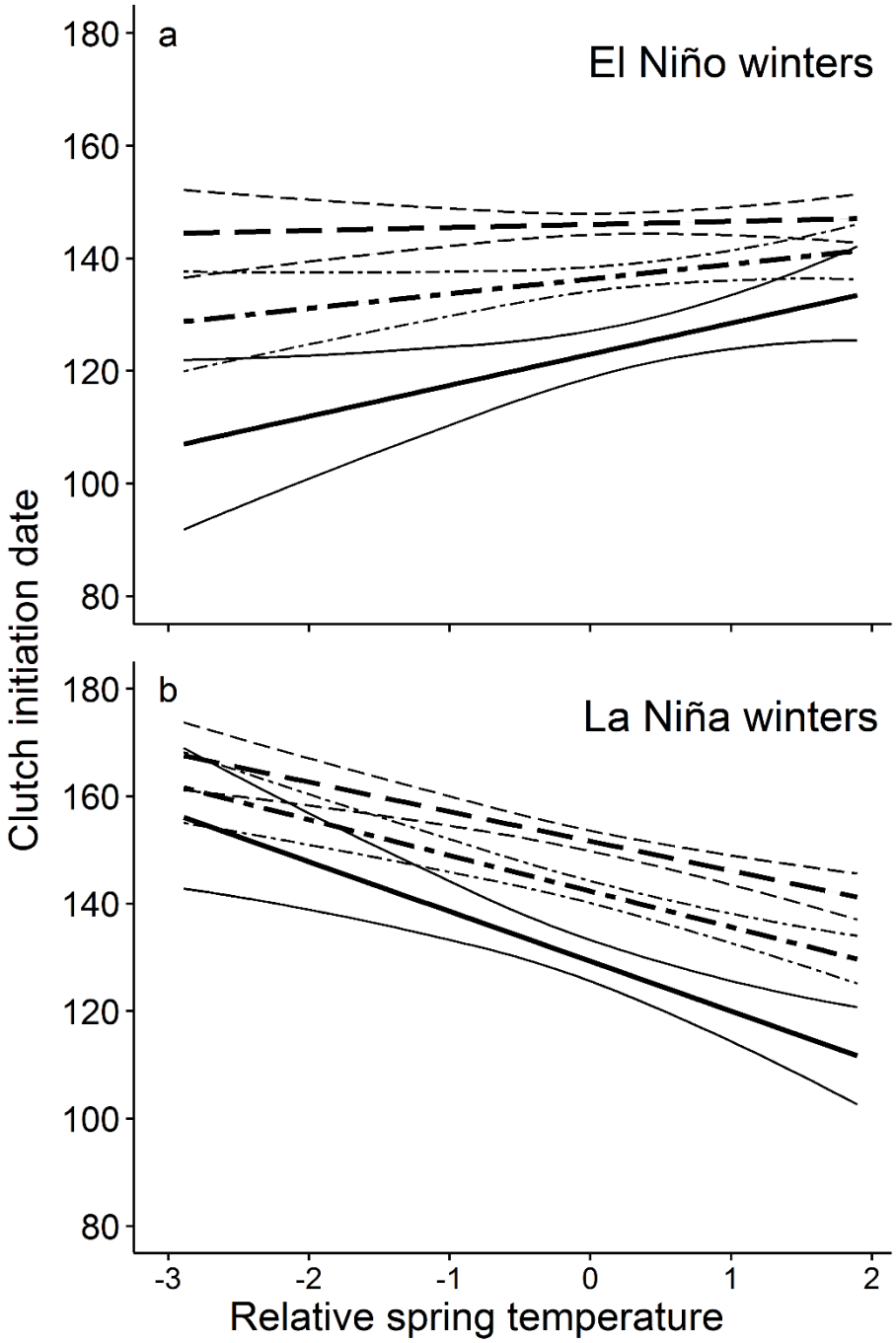


Figure 3.2 Timing of nesting (± unconditional 95% CI; days since 1 January) estimated from each species' best-approximating mixed effects model in relation to relative spring temperature while accounting for the previous winter ENSO conditions . [a) El Niño: Winter ENSO held at +1.5; b) La Niña: Winter ENSO held at -1.5] for gadwall (long dash), blue-winged teal (dot dash), and mallard (solid). Parameter estimates ± SE for each species are given in Table 3.4.



CHAPTER 4. DUCK ABUNDANCE RELATED TO CHANGES IN POND CONDITIONS AND HABITAT COMPOSITION, 1985-2011

4.1 INTRODUCTION

Land use change commonly results from agricultural intensification which typically simplifies and homogenizes landscapes at the expense of natural and complex ecosystems (Tschartnke et al. 2005; Medan et al. 2011). Land use changes can have differential effects on individual species from diverse taxa such that some may benefit whereas others are harmed or unaffected. These changes can reduce geographic ranges and local abundances causing local extirpations, and subsequently creating opportunity for non-native species to invade and colonize (Medan et al. 2011). Thus, most land use changes associated with agricultural intensification decrease biodiversity because of population declines and species extinctions (Medan et al. 2011).

Natural habitats within the Prairie Pothole Region (PPR) in North America have been highly modified and degraded by agriculture. Wetland drainage and conversion of native prairie grassland to cropland have been widespread, drastically altering the landscape through loss and fragmentation of habitat. This region is also highly influenced by environmental factors which may be further exacerbated in the face of land use change. Since wetter conditions result in more ponds, and duck abundance is positively correlated with the availability of ponds (Krapu et al. 1983; Johnson and Shaffer 1987; Austin 2002; Sæther et al. 2008), reductions in number of ponds or altered ecological function can have drastic impacts on duck populations. Historically, the responses of North American waterfowl populations to ponds have been species-specific in that densities of mallard (*Anas platyrhynchos*), northern shoveler (*A. clypeata*; hereafter "shoveler"), northern pintail (*A. acuta*; hereafter "pintail"), and blue-winged teal (*A. discors*) strongly correlate with pond densities, whereas gadwall (*A. stepera*), and American wigeon (*A. americana)* have not (Johnson and Grier 1988; Austin 2002). Consequently, it is important to consider the effects of changing pond conditions on populations of species individually, since varying levels of water support different wetland vegetation communities which in turn may favor certain duck species over others (Murkin et al. 1997).

Changing wetlands are especially important since duck species have unique affinities for different pond types. For example, densities of dabbling duck species were highest on temporary and seasonal wetlands, but blue-winged teal were also abundant on ephemeral wetlands, and pintail, green-winged teal, shoveler, and American wigeon densities were high on tilled wetlands (Kantrud and Stewart 1977).

Duck population sizes are not only correlated with pond abundances, but reproductive success tends to be positively correlated with spring wetland abundance. Nest success of dabbling duck species is positively correlated with pond density (Drever et al. 2007; Walker et al. 2013*b*) and May pond counts (Howerter et al. 2014). Furthermore, Walker et al. (2013*a*) demonstrated that brood occupancy of wetlands increased in larger wetlands with greater amounts of permanent cover for the five most common dabbling ducks (mallard, gadwall, blue-winged teal, pintail, and shoveler) breeding on the prairies. Not only does brood occupancy increase with better wetland conditions, but Bloom et al. (2012) demonstrated that mallard duckling survival was highest when broods were raised in areas with a greater proportion of wetlands with adequate, concealing vegetative cover. Thus, to reveal impacts on the duck community, it is important to determine how wetlands have changed over time as a result of changes in surrounding land use, especially loss of wetlands due to agriculture conversion (Bartzen et al. 2010).

Upland habitats adjacent to wetlands provide the primary nesting sites for many waterfowl species in the PPR, especially dabbling ducks. As a result of land use change due to agricultural impacts, large tracts of native grassland prairies have been altered resulting in changes in habitat composition (e.g., Klett et al. 1988). This has had subsequent effects on the reproductive success of ducks breeding in the PPR. Numerous studies have shown that nest success increases in landscapes composed of higher proportions of grassland habitat (e.g., Stephens et al. 2005; Bloom et al. 2013) and herbaceous cover (e.g., Howerter et al. 2014). Accordingly, studies have also reported lower nest success in heavily cropped landscapes (Greenwood et al. 1995; Drever et al. 2007; Bloom et al. 2013). Furthermore, Emery et al. (2005) demonstrated that early-season nest success was higher in planted cover, which has implications for higher offspring recruitment (Blums et al. 2002).

Not only are reproductive vital rates of waterfowl affected by changes in land use, but these changes also affect the frequency of species nesting in these habitats. Overall, Cowardin et

al. (1985) found a higher frequency of mallard nests in grassland compared to cropland habitats. However, Greenwood et al. (1995) studied multiple species and found that mallard, gadwall, and pintail nests occurred more often in native grassland, whereas blue-winged teal nested most frequently in road rights-of-way, and shoveler in hayfields and untilled uplands. This variability in selecting habitats further supports the need to consider species-specific responses to changes in upland land use.

4.1.1 Hypotheses and Predictions

Because duck reproductive success is closely associated with pond conditions and surrounding upland nesting habitat, I wanted to test whether changes in either ponds or upland habitat (e.g., loss or degradation especially due to agricultural intensification) were the most influential factors determining duck abundances in the Canadian PPR from *circa* 1985 to *circa* 2011. I focused on pintail, because of conservation concerns, mallard, because of its importance in North American duck harvests, and blue-winged teal and shoveler because of their increasing population trends within the region. The land use change hypothesis states that species may have different responses to changes in habitat area over this time period resulting in different population trajectories. Furthermore, changes in upland habitat which typically alter nesting cover could be more favorable for some species than others. If a landscape is primarily composed of a disproportionate type of upland habitat (e.g., cropland) this may favor certain species over others and result in differential reproductive success.

Because species such as blue-winged teal and shoveler have experienced large population increases during this time period, as compared to mallard and pintail, I predict that these species will be more influenced by increases in ponds. Furthermore, changes in upland habitat that have created more permanent cover may benefit all species, however, blue-winged teal and shoveler may benefit more because of their affinities for non-native herbaceous cover as compared to mallard and pintail (Greenwood et al. 1995). Additionally, conversion of woody vegetation to herbaceous cover in parkland areas could favor settling by breeding pairs of blue-winged teal, and shoveler but not mallard (Clark and Shutler 1999; Howerter et al. 2014).

4.2 METHODS

4.2.1 Land Use Change Data

Wetland and upland habitat change information was collected on 153 monitoring transects in 1985 (Millar 1987), *circa* 2001 (1999, 2001-2003), and *circa* 2011 (2008-2011,

2013) as part of a Canadian prairie habitat monitoring program (Watmough et al. 2002; Watmough and Schmoll 2007). Each transect is 19.2 km long and consists of a systematic sampling regime of alternating quarter-sections (north and south of the transect mid-line). Habitat polygons defining wetland and upland characteristics were delineated in each quarter-section using magnifying stereoscopes on air photos. Wetland classifications included cultivated, grass/sedge, wooded, deep marsh, open water, and artificial. Upland classifications included natural grassland, tame pasture, trees, low shrub, shelter belt, annual crop, and resource extraction (Watmough et al. 2002; Watmough and Schmoll 2007). To increase the potential for detecting changes in land use, I compared land use and pond characteristics from the earliest (*circa* 1985) and most recent (*circa* 2011) time periods.

4.2.2 Indexing Habitat Change

First, quarter-section level habitat data were aggregated to the segment level. I focused on four main upland habitat categories which ducks frequently use for nesting (natural grass [NATGR], crop, tame grass [TAMEG], woody cover [WOODYCOV; sum of trees and low shrubs]). I calculated the percent of each of these habitat categories on each segment for each time period. To test for differences in the mean percentage of each habitat category during each time period, I used paired sample t-tests with a Bonferroni adjustment for multiple comparisons. To calculate an absolute percent change for the two temporal extents, I subtracted the percentage of each habitat category in the 1985 period from the percentage in 2011 period. I also calculated relative percent changes (absolute percent change divided by baseline percent multiplied by 100) to test which metric would be most appropriate for detecting changes over this time period.

4.2.3 Breeding Bird and Pond Data

The U.S. Fish and Wildlife Service (USFWS)/Canadian Wildlife Service (CWS) Waterfowl Breeding Population and Habitat Survey has been conducted in May to estimate duck populations (since 1955) and assess pond conditions (since 1961 in Canada) in major North American breeding grounds. In the PPR, the aerial portion of the survey consists of a two-person crew that systematically surveys 400-m wide transects across the breeding grounds. The survey also consists of ground segments that provide additional information for calculating visibility correction factors for the aerial component, and more reliably estimate waterfowl breeding populations. As part of the ground component of this survey, crews of 2-4 people survey portions of the aerial transects to identify and count all waterfowl. Additionally, the ground crew indicates

the social status of birds and assigns them to specific ponds while also collecting data on pond type and water level stage (USFWS and CWS 1987). Total indicated breeding bird [(lone males + pairs + flocks) * 2] counts and number of ponds (i.e., wetland basins holding water) were acquired for three years (centered on survey year of habitat data ±1 year) corresponding to the quarter-sections that have habitat data for air-ground segments (Fig. 4.1; n= 42; B. Bartzen, CWS). I took the mean indicated breeding bird and pond counts for the three year period to reduce bias of anomalous years or missing data. I then calculated the change in three-year mean abundance from 1985 to 2011.

4.2.4 Testing Effects of Habitat Change on Duck Abundance

Appropriate model structures were determined by comparing diagnostic plots of preliminary models. In exploratory steps, I tested models using relative percent change and others including baseline percentages with absolute change models; however, results and conclusions were similar so I focused my analyses on absolute percent changes. Using general linear models in program R version 3.2.4 (R Core Team 2013), I began by conducting an overall analysis of the effects of habitat change on duck abundance over the full temporal extent, 1985 to 2011. Because duck abundance is highly correlated with pond abundances (Krapu et al. 1983; Johnson and Shaffer 1987; Austin 2002, Sæther et al. 2008), I first tested the effects of change in pond counts, and species-specific differences in relation to ponds. I was specifically interested in testing for species-specific differences in how duck abundances were related to pond counts. I then tested for any spatial effects such as ecoregion (i.e., grassland vs. parkland) or province (i.e., Alberta, Saskatchewan, Manitoba), including species-specific effects (spatial variable * species) and spatial differences in pond counts (spatial variable * change in pond counts). After I found the best-approximating model accounting for these effects, I then tested for any additional effects of changes in upland habitat on changes in duck abundance. I focused on changes in natural grass (NATGR), crop (CROP), tame grass (TAMEG), and woody cover (WOODYCOV). Crop and tame grass categories were inversely correlated ($r = -0.78$, $p < 0.001$, $n = 42$) so these were never included in the same model.

Because species-specific responses were evident, I then ran analyses for each species separately to determine the importance and magnitude of effects. Again I tested for effects of change in ponds, changes in the land use categories, and differences between ecoregions. I used an information theoretic approach to model selection in all analyses, comparing and ranking

models using Akaike's Information Criterion corrected for sample size (AIC_c; Burnham and Anderson 2002).

4.3 RESULTS

4.3.1 Habitat Change

The greatest absolute change in habitat from 1985 to *circa* 2011 was an increase in tame grass, with up to ~41.25% more than the previous period; average change was a ~11.84% (SD = 10.60) increase. An increase in tame grass was associated with losses in cropland area (Fig. 4.2). Natural grass and woody cover exhibited small percent changes on most segments with averages of -0.96% (SD = 1.57) and -0.27% (SD = 5.50), respectively. Between ecoregions, the greatest increases in tame grass area occurred in grasslands (range = -3.07 to +41.25%) compared to the parklands (range = 0 to +29.35%). As expected, the greatest loss of woody cover occurred in the parklands (range = -30.7 to +0.01%) versus grasslands (range = -2.10 to +0.23%; Fig. 4.3).

Comparisons of habitat composition between the three time periods show consistent trends. Differences in percent NATGR were negative and evident between all three time periods indicating a loss in the percentage of native grass. Positive changes in TAMEG between all three time periods suggest overall increases in tame grass; however, increases appear to be greater from 1985 to *circa* 2001 than from *circa* 2001 to *circa* 2011. Percent crop decreased across all three time periods; however, this decrease was more pronounced from 1985 to *circa* 2001 than from 2001 to *circa* 2011. Overall, no change in woody cover was detected between any time period, but this may be due to low sample size and high spatial variation in losses, especially in the parklands. There were no differences in pond counts from 1985 to *circa* 2001 or 2001 to *circa* 2011, but there was an overall increase in ponds from 1985 to *circa* 2011 (Table 4.1).

4.3.2 Effects of Habitat Change on Duck Abundance

Overall, there was little evidence of any effect of upland habitat change on change in duck abundance. The best-approximating model included a species * change in ponds interaction, and a change in ponds * ecoregion interaction (Table 4.2). Generally, increases in ponds resulted in more ducks ($\beta = 0.99$, SE = 0.22). However, relative to mallard (intercept value), this increase was more pronounced for blue-winged teal ($\beta = 0.61$, SE = 0.31), slower for northern pintail ($\beta = -0.70$, SE = 0.31), and similar for northern shoveler ($\beta = -0.08$, SE = 0.31). In general, there were fewer ducks in the parkland ecoregion ($\beta = -7.15$, SE = 2.76), even with increases in ponds (change in ponds * ecoregion interaction; $\beta = -0.52$, SE = 0.25). Because the

overall analysis provided evidence for species-specific responses to changes in ponds, I tested each species individually.

Blue-winged teal - There was strong evidence for a positive effect of change in ponds on changes in teal abundance ($\beta = 1.46$, SE = 0.24). And while there was some model selection uncertainty, results indicated some importance of land use changes such that decreases in crop ($\beta = -0.46$, SE = 0.23) or increases in tame grass ($\beta = 0.46$, SE = 0.25) resulted in an increase in teal (Table 4.3).

Mallard - The best-approximating model included positive effects of change in ponds ($\beta = 0.86$, SE = 0.24) on change in abundance (Table 4.3). The next competitive model included effects of ecoregion, but this parameter was not well estimated and this model did not out-compete an intercept-only model.

Northern shoveler - Change in abundance was estimated well with change in pond numbers ($\beta = 0.77$, SE = 0.24) and differences between ecoregions ($\beta = -14.38$, SE = 5.30). Increases in ponds resulted in higher shoveler abundances and, overall, there were smaller changes in shoveler abundances in the parklands compared to the grasslands (Table 4.3).

Northern pintail - The best-approximating model for pintail included ecoregion ($\beta = -9.81$, SE = 3.35) indicating that changes in abundance were smaller in the parkland as compared to the grassland (Table 4.3). Changes in pintail counts were unrelated to changes in pond abundances.

4.4 DISCUSSION

4.4.1 Habitat Change

Overall, the greatest changes in habitat in the Canadian PPR from 1985 to *circa* 2011 were observed as changes from crop to tame grass or pasturelands which is a direct result of the increase in demand for beef and the need for more pastures and forage land. Additionally, the region continued to lose natural grasslands and woody vegetation, which may be partly due to an expansion of agriculture operations in the parkland/boreal transition region (PHJV 2014). In terms of ecoregion differences, greater increases in tame grass occurred in the grasslands ecoregion compared with the parklands, and greater losses of woody cover occurred in the parklands, which is intuitive based on the types of natural cover characteristic of these regions. Although changes in land use were still occurring, about 60% of this region had already been in

cultivation by 1985, meaning that the some of the most drastic changes had already occurred (Watmough and Schmoll 2007).

When considering differences in upland habitat composition between all three time periods to examine when the greatest changes occurred, it appears that most changes occurred prior to *circa* 2001. Differences in tame grass were greatest from 1985 to *circa* 2001 compared to *circa* 2001 to *circa* 2011, which is a result of increased international competitiveness of Canada's beef markets which soared throughout the 1990s but suffered with the discovery of mad cow disease in 2003 (Sarker and Ratnasena 2014). Beef industry expansion favored increases in pasturelands to raise cattle, most likely due to conversion of cultivated lands which saw greater losses from 1985 to *circa* 2001 than *circa* 2001 to *circa* 2011. Differences in the decrease in natural grass appear consistent across all three time periods and may have been primarily due to "squaring the field", meaning that typically only small native grassland tracts were lost in a given area (Watmough and Schmoll 2007).

4.4.2 Habitat Change and Duck Abundance

When testing for species-specific responses to changes in upland habitat and ponds, there was limited evidence for any effect of changes in uplands. However, duck species responded distinctly to changes in ponds, and changes in ponds were different in each ecoregion. In general, ducks tend to track pond abundances (Krapu et al. 1983; Johnson and Shaffer 1987; Austin 2002; Sæther et al. 2008), with some differences between species. Increases in ponds in the parkland ecoregion had less impact on duck numbers than increases in the grasslands possibly because parkland ponds are more stable and tend to have greater permanency than those in the grasslands.

In the overall analysis, increases in ponds tended to increase blue-winged teal abundance more rapidly than the other three species. When pond abundance increases in the prairies, perhaps relatively more are seasonal, temporary, or even ephemeral ponds. These types of ponds not only tend to have the highest densities of blue-winged teal, overall, but ephemeral wetlands, specifically, are dominated by high number of blue-winged teal compared to other species (Kantrud and Stewart 1977). The individual species analysis for blue-winged teal confirmed the close association between pond and teal abundances. This analysis also suggested that teal abundance increased in areas where decreases in crop were recorded (primarily due to increase in tame grass across this time period). Blue-winged teal prefer to nest in grass and hayland more so

than mallard, with greatest preference for rights-of-way, suggesting that this species may be less reliant than other species on native herbaceous or woody vegetation for suitable nesting habitat (Greenwood et al. 1995). On balance, it seems most likely that blue-winged teal responded to an increase in tame grass (and ponds) during this period, owing to greater availability of suitable nesting habitat.

Change in mallard abundance was primarily driven by the change in ponds. This suggests that either ponds are the most influential factor determining population dynamics for this species or, more likely, some other factor not included in this analysis is an important driver for this species. It is not surprising that increases in tame grass over this period were not correlated with increases in mallard abundance. Mallards prefer brushy nesting habitat with almost 50% of nests recorded in this habitat during a study across the PPR in the 1980s (Greenwood et al. 1995; Howerter et al. 2008). Although area of woody cover tended to decline from 1985 to *circa* 2011, and tame grass increased, these changes in nesting habitats apparently were insufficient to alter mallard abundance.

The overall analysis detected similar responses as mallard for shovelers relative to changes in ponds. The individual analysis for shovelers provided comparable effect sizes for both species, again indicating that in general an increase in ponds resulted in higher shoveler abundance. Ecoregion was also important indicating that overall there were smaller changes in shoveler abundance in the parkland when compared to the grassland. It is surprising, however, that increases in tame grass over this period did not increase shoveler abundance. Shovelers prefer nesting in haylands more than other species (Greenwood et al. 1995). This suggests then that the increases in overall shoveler abundance over this time period (USFWS 2015) could result from other factor(s).

Pintail appeared to be less responsive to changes in ponds when compared to the other duck species. This result was further corroborated in the individual species analysis for pintail which showed no effect of change in ponds on changes of abundance for this species (i.e., change in pond did not rank higher than an intercept-only model). This phenomenon has long been documented for pintail after the drought in the prairies in the 1980s. It is most plausibly explained by decreased reproductive success due to changes in upland habitat that resulted in loss and fragmentation of nesting habitat and therefore decreased nest success (Miller and Duncan 1999; Podruzny et al. 2002). The only effect that deemed important for pintail was

ecoregion, suggesting overall smaller increases in pintail in the parkland as compared to the grassland which is consistent with the observation that pintail densities tend to be higher in the prairie compared to parkland regions (Johnson and Grier 1988).

Despite substantial changes in upland habitat between 1985 and *circa* 2011, these landscape changes had limited impacts on the species considered. Blue-winged teal responded more strongly to ponds and only teal numbers rose in areas where increases in tame grass were recorded. However, for mallard and shoveler, no additional effects of changes in upland habitat above those observed for increases in ponds appear to be influential in driving abundances of breeding pairs in these species. Therefore, observed increases in at least shoveler over this time period (USFWS 2015) cannot be attributed to land use changes and therefore may be a result of other environmental factors or due to the limited number of samples and spatial extent, I was unable to detect a response. It is also concerning that pintail did not respond to ponds or land use changes over this period. Other studies may consider conducting analyses to detect effects of land use change at other, smaller, spatial scales, or if available, earlier time periods before the landscape had already been drastically altered. Furthermore, studies that cover greater spatial extents may be better equipped to detect responses of pintails.

4.5 TABLES

Table 4.1 Paired t-tests results [t-value (p-value)] for differences in percent of each habitat category between three time periods: 1985, *circa* 2001, *circa* 2011. P-values were adjusted for multiple comparisons using Bonferroni correction factors. All comparisons used 41 degrees of freedom.

	Comparisons		
Habitat*	1985 vs. 2001	2001 vs. 2011	1985 vs. 2011
% NATGR	-3.014 (0.013)	-3.260 (0.007)	-3.958 (0.001)
% TAMEG	7.392 (<0.001)	3.015 (0.013)	7.237 (<0.001)
% CROP	-4.029 (<0.001)	-2.471 (0.053)	-5.064 (<0.001)
% WOODYCOV	-1.703 (0.288)	-2.032 (0.146)	-2.050 (0.140)
# PONDS	1.781 (0.247)	0.643 (1.00)	3.134 (0.010)

* NATGR, natural grass; TAMEG, tame grass; CROP, annual crop; WOODYCOV, woody cover; # PONDS, 3-year mean pond abundance

Table 4.2 Model selection table for change in duck abundance in relation to change in ponds (ΔPONDS), ecoregion, and effects of percent change in area of each habitat: natural grass (Δ%NATGR), crop, tame grass (Δ%TAMEG), and woody cover (Δ%WOODYCOV). Interactions also include main effects of parameters.

Model Structure	K[†]	Log likelihood	AIC_c[‡]	ΔAIC_c[§]	ω_i[‖]
SPECIES * ΔPONDS + ECOREGION * ΔPONDS	11	-694.52	1412.7	0.00	0.34
SPECIES * ΔPONDS + ECOREGION * ΔPONDS + Δ%WOODYCOV	12	-693.83	1413.7	0.94	0.21
SPECIES * ΔPONDS + ECOREGION * ΔPONDS + Δ%TAMEG	12	-694.37	1414.7	2.01	0.12
SPECIES * ΔPONDS + ECOREGION * ΔPONDS + Δ%NATGR	12	-694.46	1414.9	2.20	0.11
SPECIES * ΔPONDS + ECOREGION * ΔPONDS + Δ%CROP	12	-694.47	1414.9	2.21	0.11
SPECIES * ΔPONDS + ECOREGION	10	-696.85	1415.1	2.37	0.10
SPECIES * ΔPONDS	9	-705.09	1429.3	16.58	0.00
SPECIES + ΔPONDS	6	-713.15	1438.8	26.09	0.00
SPECIES	5	-733.89	1478.2	65.42	0.00
(intercept only)	2	-738.38	1480.8	68.10	0.00

[†] Number of parameters included in the model.

[‡] Akaike's Information Criterion corrected for sample size (AIC_c).

[§] Difference in AIC_c (ΔAIC_c) values between each model and the model with the lowest AIC_c are given.

[‖] The Akaike weight (ω_i) or likelihood of a model, given the set of models.

Table 4.3 Model selection table for individual species analyses of change in duck abundance related to change in ponds (ΔPONDS), ecoregion, and effects of percent change in area of each habitat: natural grass (Δ%NATGR), crop, tame grass (Δ%TAMEG), and woody cover (Δ%WOODYCOV).

Species/Model Structure	K[†]	Log likelihood	AIC_c[‡]	ΔAIC_c[§]	ω_i[‖]
Blue-winged teal					
ΔPONDS + Δ%CROP	4	-177.36	363.8	0	0.30
ΔPONDS + Δ%TAMEG	4	-177.60	364.3	0.49	0.23
ΔPONDS	3	-179.35	365.3	1.54	0.14
ΔPONDS * ECOREGION	5	-176.89	365.5	1.66	0.13
ΔPONDS + ECOREGION	4	-178.29	365.7	1.88	0.12
ΔPONDS + Δ%NATGR	4	-179.24	367.6	3.77	0.05
ΔPONDS + Δ%WOODYCOV	4	-179.24	367.6	3.77	0.05
(intercept only)	2	-192.47	389.3	25.46	0.00
ECOREGION	3	-191.89	390.4	26.63	0.00
Mallard					
ΔPONDS	3	-178.33	363.3	0	0.29
ΔPONDS + ECOREGION	4	-177.20	363.5	0.18	0.26
ΔPONDS + Δ%TAMEG	4	-178.22	365.5	2.22	0.09
ΔPONDS + Δ%CROP	4	-178.22	365.5	2.23	0.09
ΔPONDS * ECOREGION	5	-177.00	365.7	2.37	0.09
ΔPONDS + Δ%WOODYCOV	4	-178.33	365.7	2.44	0.09
ΔPONDS + Δ%NATGR	4	-178.33	365.7	2.44	0.09
(intercept only)	2	-184.00	372.3	9.02	0.00
ECOREGION	3	-183.12	372.9	9.58	0.00
Northern pintail					
ECOREGION	3	-158.33	323.3	0	0.54
ΔPONDS + ECOREGION	4	-157.78	324.6	1.34	0.28
ΔPONDS * ECOREGION	5	-157.41	326.5	3.20	0.11
(intercept only)	2	-162.40	329.1	5.81	0.03
ΔPONDS	3	-161.93	330.5	7.20	0.02
ΔPONDS + Δ%TAMEG	4	-160.99	331.1	7.78	0.01
ΔPONDS + Δ%CROP	4	-161.40	331.9	8.58	0.01
ΔPONDS + Δ%NATGR	4	-161.64	332.4	9.07	0.01
ΔPONDS + Δ%WOODYCOV	4	-161.89	332.9	9.58	0.01
Northern shoveler					
ΔPONDS + ECOREGION	4	-177.06	363.2	0	0.56

ΔPONDS * ECOREGION	5	-176.40	364.5	1.26	0.30
ΔPONDS	3	-180.69	368	4.80	0.05
ΔPONDS + Δ%NATGR	4	-180.35	369.8	6.58	0.02
ΔPONDS + Δ%WOODYCOV	4	-180.51	370.1	6.90	0.02
ΔPONDS + Δ%CROP	4	-180.52	370.1	6.91	0.02
ΔPONDS + Δ%TAMEG	4	-180.69	370.5	7.25	0.02
ECOREGION	3	-182.00	370.6	7.43	0.01
(intercept only)	2	-184.95	374.2	11.00	0.00

† Number of parameters included in the model.

‡ Akaike's Information Criterion corrected for sample size (AIC_c).

§ Difference in AIC_c (ΔAIC_c) values between each model and the model with the lowest AIC_c are given.

‖ The Akaike weight (ω_i) or likelihood of a model, given the set of models.

4.6 FIGURES

Figure 4.1 Segment-level (n = 42) distributions of 3-year mean abundance at each time period (1985, *circa* 2001, and *circa* 2011) of pond counts (PONDS) and total indicated breeding birds of each species: blue-winged teal (BWTE), mallard (MALL), northern pintail (NOPI), and northern shoveler (NSHO). Distributions are represented by box (25^{th}, 50^{th} [median], and 75^{th} quantiles) and whisker (1.5 * IQR [75^{th} -25^{th} quantile]) plots. Any points beyond each whisker are values greater than 1.5*IQR.

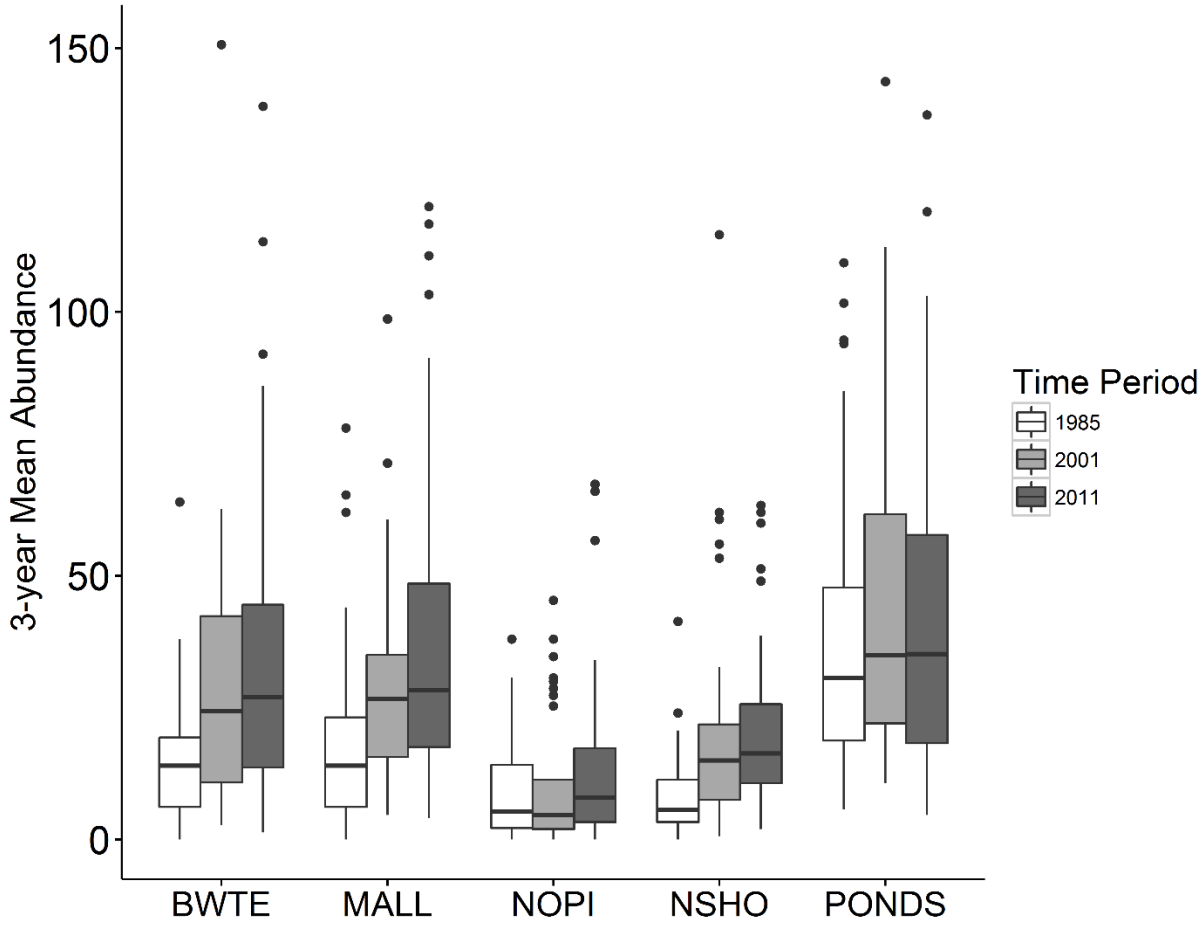


Figure 4.2 Absolute percent change in area of each habitat category across all segments from 1985 to *circa* 2011 (n = 42). Distributions are represented by box (25^{th}, 50^{th} [median], and 75^{th} quantiles) and whisker (1.5 * IQR [75^{th} -25^{th} quantile]) plots. Any points beyond each whisker are values greater than 1.5*IQR. NATGR = natural grass; TAMEG = tame grass; CROP = annual crop; WOODYCOV = woody cover.

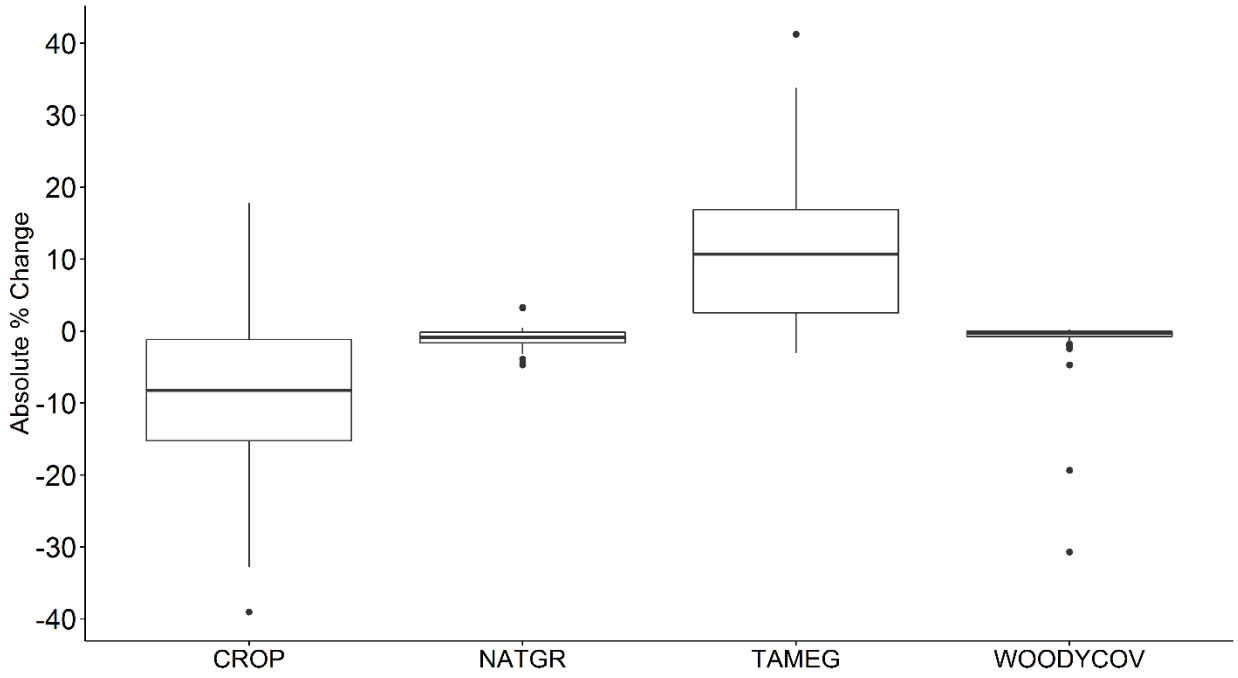
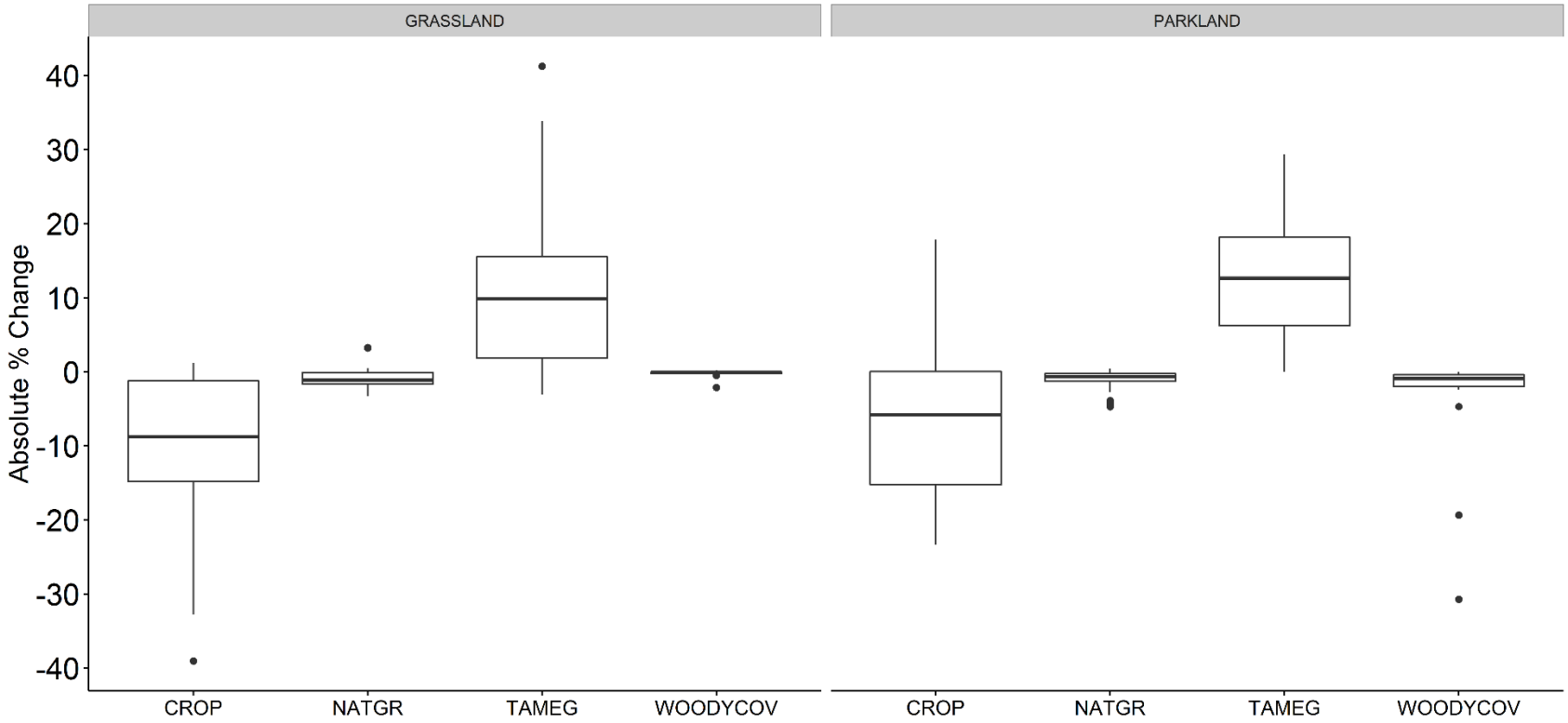


Figure 4.3 Absolute percent change in area of each habitat category by ecoregion (grassland, n = 24; parkland, n = 18) from 1985 to *circa* 2011. Distributions are represented by box (25^{th}, 50^{th} [median], and 75^{th} quantiles) and whisker (1.5 * IQR [75^{th} -25^{th} quantile]) plots. Any points beyond each whisker are values greater than 1.5*IQR. NATGR = natural grass; TAMEG = tame grass; CROP = annual crop; WOODYCOV = woody cover.



CHAPTER 5. SYNTHESIS

Shifts in the duck community composition in the Prairie Pothole Region of Canada (PPR) have been evident over the past 25 years with several, previously untested explanations for species-specific population trends. Abundances of blue-winged teal, shoveler, and gadwall have increased dramatically, with a decline in pintail (USFWS 2015, Chapter 2). Since the 1800s, the climate has warmed 0.85ºC with projected increases of 0.3 to 0.7ºC over the next two decades (Kirtman et al. 2013). Warmer temperatures will have implications for pond persistence, composition and function (Larson 1995; Millet et al. 2009) and for ducks that rely so heavily on these wetland systems (Krapu et al. 1983; Johnson and Shaffer 1987; Austin 2002; Sæther et al. 2008). Changes in climate will also trigger further modifications in land use that have been occurring in this region for decades, especially with drying wetland basins (Bartzen et al. 2010). This region has been heavily dominated by cultivation (Watmough and Schmoll 2007), however, since the 1980s it has seen a conversion of cropland to pasturelands as a result of the strengthening cattle industry (Sarker and Ratnasena 2014). My research has attempted to test the relative importance of some of these factors as drivers of duck species populations in the PPR.

To test the neutral hypothesis that shifts in duck species populations were merely a result of movements among regions, in Chapter 2, I tested for redistribution using correlations and synchrony between population abundances for the Canadian PPR, U.S. PPR, and southern boreal forest from 1974 to 2014. I predicted that if negative correlations or asynchrony were evident for populations between two regions, this would be consistent with redistribution among regions for a species. Then, I modelled populations of each species between the U.S. and Canadian PPR to test for differential responses to region-specific pond counts. I found very little evidence to support this idea (Table 5.1). Blue-winged teal was the only species that exhibited any negative correlation, however, this was between the U.S. PPR and southern boreal forest, the latter of which only supports 10% of this species' North American population (USFWS 2015). Redhead was the only species to exhibit asynchrony between two regions, but subsequent modeling exercises suggested that regional redhead populations were responding to region-specific pond counts. From the modelling analysis, mallard, blue-winged teal, and redhead were the only species that showed a response to region-specific ponds counts, however, estimates of these responses were positive indicating similar responses in both regions for all three species. Overall,

I detected limited evidence for redistribution for explaining differences in species population trajectories in the Canadian PPR.

In Chapter 3, I examined species-specific responses in timing of nesting and subsequent nest survival to variations in current-year spring weather and antecedent winter climate conditions as mechanisms that might explain different population patterns exhibited by each species. I predicted that females would nest earlier following wetter winters and warmer springs which would lead to higher nest survival; however, I also reasoned that the ability of a species to respond would be related to its innate flexibility in breeding chronology. I only felt confident in drawing conclusions about the results for species with adequate sample sizes (i.e., mallard, blue-winged teal, northern shoveler, gadwall, and northern pintail). For these species, I found that in general nesting was earlier in warmer springs and following wetter winters, with the exception of pintail which did not respond to winter climate conditions. Responses for all species had different effect sizes indicating species-specific responses. Moisture conditions on the breeding grounds were also important for pintail and shoveler by shifting distributions of nest initiations later presumably due to higher renesting rates or more nest attempts by younger females. I found weak evidence that increases in temperature result in higher nest survival for shoveler, gadwall, and mallard (Table 5.1). Most species, with the exception of pintail and shoveler, demonstrated strong date effects on nest survival and were able to adjust their nesting dates in response to the climate conditions. Therefore, if timing of nesting varies with climate and nest survival varies with timing, this may provide a mechanism by which cross-seasonal effects and differential responses to spring phenology can impact duck population dynamics.

In Chapter 4, I tested whether changes in pond availability or habitat composition from 1985 to *circa* 2011 influenced changes in abundance of mallard, pintail, shoveler, and blue-winged teal. Because the greatest increases in abundances between these periods were recorded for shoveler and blue-winged teal (Chapter 2), I predicted that these species would be most responsive to beneficial changes in pond abundance or land use. I found that the greatest change in upland land use was a shift from crop to tame grass, but there was only a weak association between abundances of blue-winged teal and these land use changes. No other species demonstrated any effect of change in land use on change in abundance. The most important factor was change in ponds for all species except pintail (Table 5.1). Overall, changes in land use

over this period did not seem to be very important drivers of population trends, given sample sizes and the spatiotemporal scale examined in my study.

To conclude, my work provides insights into possible drivers and mechanisms of species population trends but cannot fully explain increases in blue-winged teal, shoveler, and gadwall as compared to mallard and especially pintails (Table 5.1). In general, species appear to be most responsive to variations in climate (Chapter 3), however, I did not directly test whether these responses affected population abundances so there are still some questions to be answered there. The sole response of blue-winged to changes in land use (Chapter 4) could provide some explanation for why this species has increased over this time period, but this still does not explain increases in shoveler or gadwall populations. Pintail, on the other hand, have been at low population levels over this time period and do not seem to show strong responses to any factors considered. Lastly, redistribution seems like an unlikely explanation (Chapter 2) due to the fact that there would have to have been a large exodus of a species' population that would be hard to attain merely due to the large sizes of these populations in general.

5.1 MANAGEMENT IMPLICATIONS AND FUTURE RESEARCH

Discovering species-specific responses to variations in climate is an important finding, especially when it appears that most species have some capability of adjusting nesting activities in response to such variations. This is reassuring especially with the predicted warming for this region (Kirtman et al. 2013) and my finding that nest survival is higher in warmer temperatures for certain species suggests that some species may be able to thrive or at least sustain populations, at least in the short-term. Another consideration would be to focus on changes in precipitation patterns over this period. Climate studies have demonstrated that the amount of precipitation falling as snow has decreased over time (Vincent et al. 2015) which may have implications for the success of later vs. earlier nesting species. Later rains throughout the breeding season may increase available brood-rearing habitat and encourage re-nesting by late nest species, therefore, extending the nesting season (Raquel et al. 2016) and further enhancing hen success and duckling survival most among females of late-nesting species.

My research also highlights the importance of full-annual cycle modelling by considering factors on wintering and breeding grounds and allowing these to directly compete to determine the relative importance of each (see Osnas et al. 2016). Further studies should continue to

consider factors at different stages of the annual cycle, with more work needed on factors experienced on migration and at stopover locations. Although, I found the strongest responses to climate variables compared with land use, this is troubling from a management perspective because climate cannot be controlled whereas land use can at least be influenced by habitat management programs, and progressive agricultural, wetland and other policies.

It is encouraging that I detected some evidence for an effect of increases in tame grass, if only on one species. This implies that improvements in upland habitat could result in positive effects on pair settling in some species perhaps even offsetting negative effects of wetland loss. Furthermore, because I found few and limited responses by other species, this suggests that either these species have more specific habitat requirements such as specific preferences for certain cover types, especially for nest site preferences (Greenwood et al. 1995), or that responses for these species may not be detectable at the scale I used. Additionally, I was somewhat constrained by having only 42 transects which may not have provided an accurate depiction of changes in ducks and land use from the time period from, roughly, 1985 to *circa* 2011. Therefore future studies should attempt to test for effects of land use change with more replicates. Future studies may also want to consider responses to changes in field cultivation practices. Although I detected very little response to changes in land use, changes in ponds were an important factor for all species except pintail. This provides more strength to the argument for protecting, restoring, and preserving wetland habitats as a means to improve and sustain waterfowl populations especially in the face of predicted climate scenarios that expect further loss of wetlands in the future (Larson 1995; Millet et al. 2009).

My research further highlights the importance of both spatial and temporal extent in projects and datasets. Having data across an entire region can give stronger confidence in results especially at a population level, however, if samples are sparsely distributed across a region, there may be missing information. Furthermore, long-term datasets provide the ability to detect changes and responses over time. Therefore, long-term studies should continue, and if possible be expanded in spatial extent. This will become increasingly important in the face of expected environmental changes.

Table 5.1 Summary of species-specific responses to each of the three hypotheses tested in the thesis: (i) redistribution, (ii) climate, and (iii) land use. Within the climate hypothesis, responses to winter El Niño Southern Oscillation Index (wintENSO), spring temperature (SprT), and moisture anomaly index (MAI) are shown. If a response was detected for a species, the climate variable and direction of the response is noted by either positive (+) or negative (-) and the magnitude is indicated by multiple symbols signifying stronger responses. N.S. means the response was not significant. Blank cells indicate that no test was done for that hypothesis.

	Hypotheses				
	Redistribution	Climate		Land Use	
Species		Timing of Nesting*	Nest Survival†	Ponds	Upland Cover
Mallard (*Anas platyrhynchos*)	N.S.	(-- wintENSO; -- SprT)	(+ SprT)	(++)	N.S.
Northern pintail (*A. acuta*)	N.S.	(-- SprT; ++ MAI)	(- MAI)	N.S.	N.S.
Blue-winged teal (*A. discors*)	N.S.	(-- wintENSO; -- SprT)	(- MAI)	(++)	(+)
Northern shoveler (*A. clypeata*)	N.S.	(-- wintENSO; -- SprT; ++ MAI)	(+ SprT)	(++)	N.S.
Gadwall (*A. strepera*)	N.S.	(-- wintENSO; -- SprT)	(+ SprT)		
American green-winged teal (*A. carolinensis*)	N.S.	(- SprT)	N.S.		
American wigeon (*A. americana*)	N.S.	(- SprT)	(+ SprT)		
Lesser scaup (*Aythya affinis*)	N.S.	N.S.	N.S.		
Canvasback (*Aythya valisineria*)	N.S.				

Redhead (*Aythya americana*)	N.S.
Ruddy duck (*Oxyura jamaicensis*)	N.S.

* Negative relationships between timing of nesting and wintENSO and/or SprT indicate earlier nesting following warmer, wetter winters and/or warmer springs. Positive responses to MAI indicate later nesting in wetter springs.

† Positive relationships of nest survival and SprT indicate higher nest survival in warmer springs whereas negative relationships with MAI indicate lower nest survival in wetter springs.

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APPENDIX A. TIMING OF NESTING OF UPLAND-NESTING DUCKS IN THE CANADIAN PRAIRIES AND ITS RELATION TO SPRING WETLAND CONDITIONS

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A.1 INTRODUCTION

Timing of breeding is an influential avian life-history trait, with substantial impacts on reproductive success. Variation in timing of breeding within a waterfowl species can affect clutch size (Lepage et al. 2000), nest success (Emery et al. 2005), and offspring survival (Sedinger and Raveling 1986; Lindholm et al. 1994; Dzus and Clark 1998; Krapu et al. 2000; Traylor and Alisauskas 2006; Gurney et al. 2012). In ducks, such differences can have consequences for eventual offspring recruitment (Blums et al. 2002), and life-time reproductive success of females (Blums and Clark 2004) which, in turn, influence population dynamics.

Differences in reproductive success and survival may be related to poorer body condition of late-breeding females that allocate less time to parental care (Sedinger and Raveling 1986; Paasivaara and Pöysä 2007), or to seasonal deterioration in wetland habitat quality (Elmberg et al. 2005), as measured by pond abundance (Rotella and Ratti 1992; Dzus and Clark 1998; Guyn and Clark 1999; Krapu et al. 2000; Gendron and Clark 2002). Duckling (Guyn and Clark 1999; Krapu et al. 2000) and brood (Rotella and Ratti 1992; Gendron and Clark 2002) survival rates are typically higher when pond abundance is high, which is often most evident in early-hatched birds.

Most descriptions of the timing of nesting for upland-nesting prairie ducks are either qualitative or uncommon for some species such as American wigeon (*Anas americana* (Gmelin, 1789); hereafter "wigeon") and green-winged teal (*A. crecca carolinensis* (Gmelin, 1789)). Mallard (*Anas platyrhynchos* (Linnaeus, 1758)) and northern pintail (*A. acuta* (L., 1758);

hereafter "pintail") are generally considered early nesters, whereas gadwall (*A. strepera* (L., 1758)) and lesser scaup (*Aythya affinis* (Eyton, 1838); hereafter "scaup") have been referred to as "late nesters" and other species as "intermediate" nesters. Specifically among prairie-nesting ducks, mallard (Drilling et al. 2002; Baldassarre 2014) and pintail (Clark et al. 2014; Baldassarre 2014) have been described as initiating nests in early to mid-April. Northern shoveler (*A. clypeata* (L., 1758); hereafter "shoveler") and blue-winged teal (*A. discors* (L., 1766)) start nesting in early May (Sowls 1955; Dubowy 1996; Rohwer et al. 2002), with green-winged teal (Palmer 1976; Johnson 1995), gadwall (Hines and Mitchell 1983; Leschack et al. 1997), and wigeon in mid to late May (Wishart 1983; Mini et al. 2014). Scaup initiate nests in late May (Stoudt 1971; Anteau et al. 2014), and similarly, white-winged scoters (*Melanitta fusca deglandi*, (Bonaparte, 1850); herafter "scoter") initiate nests in late May to early June (Brown and Brown 1981; Baldassarre 2014).

Greater uncertainty surrounds the span of nesting, the time period when most nests are initiated. Greenwood et al. (1995) characterized the average length of the nest-initiation period as the interquartile range (25–75% dates) for five duck species nesting in prairie Canada, and concluded that mallard and pintail had the longest periods of 27 and 26 days, respectively; shoveler, blue-winged teal, and gadwall had nest-initiation periods of 16, 15, and 13 days, respectively. Greenwood et al. (1995) questioned whether their results were fully representative because sites were selected in areas of high mallard densities and the three-year study was conducted during a dry period. Other studies have characterized the span of nesting for wigeon, green-winged teal, scaup, and scoter but a common set of descriptive metrics has not been used. About 88% of green-winged teal nests were initiated over a 49 day period (Emery et al. 2005; Baldassarre 2014), but nesting information about this species is limited (Guillemain and Elmberg 2014). In wigeon, 90% of nests were initiated over a 29 day period (Kruse and Bowen 1996; Mini et al. 2014). Spans of nesting for scaup and scoter have been characterized by the range between minimum and maximum nest initiation dates which range from 18–42 days for scaup (Koons and Rotella 2003; Anteau et al. 2014) and up to 42 days for scoter (Brown and Brown 1981; Baldassarre 2014). Providing more complete, consistent estimates of span of nesting is important for understanding correlates of reproductive effort on a species-specific basis. Furthermore, such information may provide useful benchmarks for future studies of comparative reproductive patterns or effects of environmental change on timing of breeding in ducks.

I quantified patterns in the timing and span of nesting for nine upland-nesting duck species in the Prairie Pothole Region of Canada. To my knowledge, this is the largest comparative study of temporal nesting patterns in a guild of upland-nesting ducks which, importantly, accounts for spatiotemporal variation in environmental conditions. I determined start, span, and end of nesting (see Methods for definitions) dates for each species. Then, I tested whether the span and end of nesting season were related to variation in habitat quality as indexed by local pond abundance (Greenwood et al. 1995). I predicted that the span and end of nesting would be positively related to May pond counts due to greater reproductive investment (including re-nesting) in years with favourable habitat for rearing offspring (Rotella et al. 2003; Arnold et al. 2010) or higher incidence of late-nesting yearling females breeding in years of favourable pond conditions (e.g., Dufour and Clark 2002).

A.2 METHODS

A.2.1 Study Areas

Long-term single-site studies were conducted at St. Denis National Wildlife Area (SDNWA; 52° 12’ N, 106° 5’ W) and at Redberry Lake (52° 42’ N, 107° 10’ W) which are about 40 km east and 80 km north of Saskatoon, Saskatchewan, respectively. SDNWA is a 361-ha area managed by Environment and Climate Change Canada and is characterized by >100 wetland basins distributed amongst patches of native grasses, shrubs, aspen groves (*Populus tremuloides* (Michx.)), and planted cover (mixed brome grass, *Bromus* (L.) spp., and alfalfa, *Medicago sativa* (L.)). Redberry Lake is a 4,500-ha federal bird sanctuary and World Biosphere reserve. Islands within the lake are dominated by various willow (*Salix* (L.) spp.), aspen, grass (*Poaceae* family) and berry species (e.g. *Ribes oxycanthoides* (L.), *Symphoricarpos occidentalis* (Hook.), *Amelanchier alnifolia* ((Nutt.) Nutt. ex M. Roem.)).

Long-term multi-site nesting data were incorporated from three studies conducted by Ducks Unlimited Canada (PHJV Assessment Study, 1993–2000 [Howerter et al. 2014]; Pintail Study, 2005–2007; and Spatial/Temporal Variability Study [SpATS], 2002–2011; hereafter “DUC sites”). There were 27 65-km^2 study sites from the Assessment study, 17 41.4-km^2 study sites from the Pintail study, and 120 41.4-km^2 study sites from the SpATS study. All study sites were located within the Canadian Prairie Pothole Region (PPR) which spans southern Alberta, Saskatchewan, and Manitoba and is characterized by flat to rolling terrain, interspersed with numerous wetland basins of varying size and pond permanency.

A.2.2 Locating Nests

At SDNWA (1980-81, 1984–2000) and the DUC sites (1993–2000, 2002–2011), I searched for nests during three to four intervals from early May to mid-July each year. Searches were usually conducted between 0700 to 1500 hr, each at three week intervals (Gloutney et al. 1993). Nests were found after flushing females from nests, either by pulling ropes or heavy cable-chains between two all-terrain vehicles in herbaceous cover, or by walking through and beating vegetation with willow switches or bamboo canes in shrub-woodland cover (Klett et al. 1986). On islands at Redberry Lake, 3 to 5 nest searches for scoters were done on foot assisted by dogs (*Canis domesticus* (L., 1758)) between 0700 and 2200 hr from early June to mid-August, 2000–2014 (Traylor et al. 2004). At each nest (bowl with ≥1 egg), duck species (scoter only at Redberry Lake) was recorded. Clutch size, estimated incubation stage (Weller 1956), and the date that each individual nest was found were recorded. Nest initiation dates were determined by assuming one egg was laid per day (except scoter, one egg every 1.5 days) and I made no adjustments for possible loss of eggs prior to discovery, assuming that it occurred infrequently and was applicable to all species. After each visit, nests were covered with nesting material to mimic normal female departures (Götmark 1992). All field protocols were reviewed and approved by the University of Saskatchewan's Animal Care Committee on behalf of the Canadian Council on Animal Care.

A.2.3 Analyses

Analyses were based on species, site and year-specific values of start (date when first 10% of nests had been initiated), span (range between dates [days] when 10 and 90% of nests had been initiated) and end (date when 90% of nests had been initiated) of nesting. In the analysis that incorporated all site-years from all studies, I used general linear mixed effects models to first characterize the start, span, and end of nesting for each species controlling for random effects of site-year. I also computed 5%, median (50%), and 95% dates as well as the interquartile range (IQR; 25–75%). To compare between studies over the same time period (1994–2000), I analyzed data separately from SDNWA only and from multiple-sites (i.e., DUC sites), using general linear mixed effects models to estimate start, span, and end of nesting by species while accounting for random effects of year and site-year, respectively. This analysis enabled me to assess how conclusions about species-specific temporal patterns of nesting might

differ in relation to spatial scale and nest-searching methods. Least-squares mean parameter estimates and standard errors were calculated for each nesting metric by species. Post-hoc multiple comparison Tukey contrasts were conducted among species for each nesting metric in the overall analysis to test for species-specific differences. Species and year or site-year combinations with less than five nests and visually extreme outliers (n = 6, site-years = 1) were excluded from all analyses, except in the case of Redberry Lake where one year with four nests was included.

I used general linear mixed effects models to test whether annual counts of May ponds and geographical location (latitude and longitude) influenced the start, span, and end of nesting. Aerial and ground portions of the U.S. Fish and Wildlife Service/Canadian Wildlife Service Waterfowl Breeding Population and Habitat Survey (WBPHS; https://migbirdapps.fws.gov) have been conducted in May of each year since 1955 to estimate the size of duck populations and wetland conditions in the prairies (USFWS and CWS 1987). Stratum-level pond counts corresponding to each site-year were acquired from this survey and were standardized (z-scores). Models incorporated independent and interactive effects of pond counts to test for species-specific responses in start, span, and end of nesting to May pond numbers; scoter was omitted because the sampled population breeds exclusively on islands at Redberry Lake, a permanent water body. Models were compared using Akaike's Information Criterion corrected for small sample size (AIC_c; Burnham and Anderson 2002) for candidate model sets based on a consistent random effects structure (i.e., site-year). Parameter estimates from the best-approximating model are presented rather than model-averaged coefficients because of weak collinearity among two predictor variables (Cade 2015). All analyses were performed using R 3.1.2 software (R Core Team 2013).

A.3 RESULTS

In total, 25 959 duck nest records from 166 sites (SDNWA [n = 3 900 nests]; Redberry Lake [n = 1 005 scoter nests]; DUC studies [n = 21 054 nests, 164 sites]) were used to quantify the start, span, and end of nesting for each species (Table A.1 gives samples sizes and complete nesting metrics for individual species). As expected, pintail and mallard were the earliest nesters overall, followed by shoveler, green-winged teal, and blue-winged teal (Fig. A.1). Wigeon and gadwall nested slightly later than shovelers and both teal species, and scaup and scoter nested the latest. Tukey tests indicated that most species differed ($p < 0.05$) in start of nesting; there were

no differences in any of the three nesting metrics between scaup and scoter or between blue-winged teal and green-winged teal. Span of nesting was similar for (i) pintail and mallard, for (ii) shoveler, blue-winged teal, and green-winged teal, and for (iii) wigeon, gadwall, scaup and scoter (Fig. A.1, Panel 1). End of nesting was distinctly early for pintail when compared with mallard, shoveler, green-winged teal, and wigeon which all ended at similar times. Blue-winged teal, wigeon and green-winged teal ended nesting at similar times. Gadwall ended nesting later than all other dabbling ducks, followed by scaup and scoter which were most similar to each other (Fig. A.1, Panel 2).

The same general patterns among species were evident in analyses that directly compared single-site versus multi-site data, 1994-2000 (sample sizes and estimates are shown in Supplementary Material A.1). Start of nesting was slightly later and span of nesting slightly longer for each species in the single-site results, but 95% confidence intervals of estimates for individual species overlapped between the two analyses (Fig. A.2). At SDNWA, differences among species estimates were less pronounced due to smaller sample sizes and corresponding overlaps in 95% confidence intervals. Timing metrics among species were more distinct in the DUC multi-site data, except for blue-winged teal and shoveler which exhibited greater overlap.

Overall, higher abundance of ponds appeared to extend the nesting season. Results indicated that species-specific responses in both span and end of nesting were related to May pond counts (start of nesting was not related to May ponds or locations, all $p > 0.44$), and end of nesting was also related to geographical location (Table A.2). Wigeon, blue-winged teal, gadwall, and shoveler exhibited positive responses in span of nesting to pond counts. Wigeon, gadwall, scaup, mallard, and shoveler showed positive responses in the end of nesting to pond counts. End of nesting also appears to be later at study sites located to the north and to the east (Table A.3).

A.4 DISCUSSION

My results demonstrated strong species-specific differences in start of nesting: mallard and pintail initiated nests earliest, followed by shoveler, the two teal species, wigeon, gadwall and, finally, scaup and scoter. My results are generally consistent with those of Greenwood et al. (1995) who considered median date as a metric for timing of nesting and reported that pintail and mallard were earliest, followed by shoveler and blue-winged teal, and then gadwall. Median nesting date may be influenced by nest success rates (Greenwood et al. 1995), so metrics like

10% or possibly 25% nest dates may be more useful indicators of the start of nesting for investigating relationships with spring climate or pond conditions. Despite differences in study-specific habitat conditions, interspecific patterns in start of nesting for each species were quite well conserved over time and across sites as shown by the direct comparison of SDNWA and DUC sites, 1994–2000. Both analyses produced comparable estimates of start date for individual species even though the DUC multi-site analyses considered nesting records from many locales, each with unique habitats. However, for each species, the multi-site estimates for start of nesting were slightly earlier than the single-site estimates which may result from latitudinal variation in duck densities and timing of nesting (Sæther et al. 2008), or other factors discussed below.

Predictably, span of nesting by each species followed a pattern similar to that of the start of nesting between species. Mallard and pintail had the longest nesting spans, followed by shoveler and both teal species, wigeon, gadwall, and finally scaup and scoter with the shortest spans. The patterns we found between species were also consistent with those of Greenwood et al. (1995), and my estimates of IQR were similar. It makes intuitive sense for a species that nests earlier in the season to have more time for re-nesting following losses of clutches or early-season broods. Pintails and mallards had a similar span of nesting, implying that female pintails may have greater re-nesting potential than has generally been assumed or some female pintails have a long period of restraint (or constraint) before egg-laying. At the single-site level, span of nesting tended to be longer for each individual species. Differences among studies in start, span, and end of nesting may result from specific habitat conditions at particular sites or differences in methodology such as at SDNWA where nest searches often continued later into the season than at the DUC sites. Likewise, in DUC's Assessment Study, timing of breeding by radio-marked mallards extended on average two days later than did mallard nests discovered by conventional nest searching methods (JHD and DWH, unpubl.). However, I suspect that the small differences between studies in start and span of nesting for individual species reflect duck responses to local environmental conditions rather than nest-searching methods because disparities between these estimates were not more pronounced for late- versus early-nesting species (Supplementary Material A.1).

Variation in the end of nesting among pintail, shoveler, mallard, blue-winged teal, and gadwall was similar to the findings of Krapu (2000), however Tukey contrasts suggested pintail ended nesting distinctly early and gadwall distinctly late, followed by scaup and scoter when

comparing amongst all species we considered. Krapu (2000) emphasized that shoveler ended nesting as early as pintail due to environmental limitations imposed on shovelers by their specialized diet of Cladocera. However, I found no differences in end of nesting estimates of shoveler compared to those of mallard, wigeon, and green-winged teal. My results also indicated that shoveler did not delay nor curtail nesting relative to other species like green-winged teal, as suggested by Dubowy (1985). Female shovelers were among the first to initiate nests, and span and end of nesting were unexceptional relative to other dabbling ducks (Fig. A.1). Shoveler, wigeon, and gadwall responded to May pond counts by nesting later and extending the span of nesting suggesting that span for these species was more a function of protracted nesting in years with more ponds. Blue-winged teal only responded to higher pond counts by extending the span of nesting whereas mallard and scaup responded by nesting later (Table A.3). Relationships between pond counts and end and span of nesting may be weakened due to higher nest and brood survival rates in wetter years, thereby reducing the renesting rate (Drever et al. 2007; Howerter et al. 2014).

The difference between the earliest and latest species in mean start of nesting was 44 days (Table A.1, Fig. A.1; 38 days if scoter is excluded) whereas the difference in mean end of nesting was 19 days (16 days without scoter). Among dabbling ducks only, these differences were 32 days and 11 days, respectively, suggesting that seasonally deteriorating environmental conditions and declining offspring recruitment may constrain late breeding dates in these species (Blums et al. 2002). The lateness of nesting by both scaup and scoter may impinge on nutritional and energetic needs of ducklings that must develop sufficiently in order to fledge before autumn migration. Scoters in particular are large-bodied ducks and so ducklings require absolutely greater resources per capita than smaller species. Perhaps these two duck species optimize timing of breeding to exploit higher biomass and abundance of key prey species (Brown and Fredickson 1986) such as amphipod crustaceans (Dawson and Clark 1996) in late summer, offsetting potential costs associated with their proclivities to nest the latest.

Differences in the span of nesting may have been more a result of local environmental conditions than was start of nesting which was unrelated to May pond counts. In general, both span and end of nesting were positively related to May pond conditions, consistent with previous work (Krapu et al. 1983; Greenwood et al. 1995). Presumably, increased pond abundance could favour breeding by younger females or more re-nesting attempts (Rotella et al. 2003; Arnold et

al. 2010), extending the length of nesting by local populations in some species more than others. For instance, early-nesting species may already have such long spans that May pond conditions have limited influence on re-nesting potential. Intermediate nesters may be opportunistic and able to take advantage of good pond conditions by actively re-nesting whereas late species typically nest so late in the season that they cannot alter their span of nesting in any way because females are already under strong time constraints to complete wing moult before normal dates for autumn migration.

Defining the timing and variability of nesting as well as obtaining new knowledge about factors that affect the length of the nesting season for each species are necessary steps for predicting whether and how breeding date may be influenced by future environmental changes. To determine the manner of species-specific responses to possible changes in prairie climate (i.e. early breeding species may be more flexible than late breeders; Drever et al. 2012), an important prerequisite is the empirical definition of nesting schedules. I quantitatively defined metrics for timing of nesting for nine upland-nesting species in the PPR of Canada which will be useful for future comparative studies. Therefore, I encourage a more complete and consistent description of nesting metrics (Table A.1) in ducks and other species to inform future (meta-) analyses of avian nesting dates. Additionally, a sound understanding of variation in nesting chronology, including the potential for facultative adjustments to such breeding schedules, could have land management implications when attempting to increase duck production in continuously farmed landscapes (e.g., Klett et al. 1988).

A.5 TABLES

Table A.1 Number of nests, number of site-years, and least squares mean (LSmean; calendar date) parameter estimates ± SE of nesting metrics for each species, combined data sets. LSmeans and SE were estimated with a mixed effects model, with fixed effects of species and random effects site-year*. Span refers to the number of days between the 10% and 90% nest dates, and IQR refers to inter-quartile range (25–75% nest dates).

Species[†]	*N*	Site-year	5% Date	10% Date	25% Date	50% Date	75% Date	90% Date	95% Date	Span (10-90%)	IQR (25-75%)
AGWT	441	33	14 May ± 1.3	15 May ± 1.3	20 May ± 1.3	29 May ± 1.3	8 Jun ± 1.2	15 Jun± 1.3	17 Jun ± 1.3	31 ± 1.5	19 ± 1.2
AMWI	586	40	21 May ± 1.2	23 May ± 1.2	28 May ± 1.2	4 Jun ± 1.2	11 Jun ± 1.1	16 Jun ± 1.2	17 Jun ± 1.2	24 ± 1.4	14 ± 1.1
BWTE	7785	173	16 May ± 0.6	18 May ± 0.6	24 May ± 0.7	1 Jun ± 0.7	10 Jun ± 0.7	17 Jun ± 0.6	20 Jun ± 0.7	30 ± 0.7	17 ± 0.6
GADW	3938	126	27 May ± 0.7	28 May ± 0.7	2 Jun ± 0.8	8 Jun ± 0.8	14 Jun ± 0.7	19 Jun ± 0.7	21 Jun ± 0.7	22 ± 0.8	13 ± 0.7
LESC	536	35	4 Jun ± 1.2	5 Jun ± 1.2	9 Jun ± 1.3	14 Jun ± 1.3	19 Jun ± 1.2	24 Jun ± 1.2	25 Jun ± 1.2	19 ± 1.5	11 ± 1.2
MALL	6677	149	2 May ± 0.7	5 May ± 0.7	12 May ± 0.7	25 May ± 0.7	6 Jun ± 0.7	14 Jun ± 0.7	17 Jun ± 0.7	40 ± 0.8	24 ± 0.6
NOPI	1379	78	27 Apr ± 0.9	29 Apr ± 0.9	6 May ± 0.9	18 May ± 0.9	31 May ± 0.9	8 Jun ± 0.9	11 Jun ± 0.9	40 ± 1.0	25 ± 0.8
NSHO	3612	138	12 May ± 0.7	14 May ± 0.7	20 May ± 0.7	28 May ± 0.7	6 Jun ± 0.7	13 Jun ± 0.7	15 Jun ± 0.7	29 ± 0.8	17 ± 0.6
WWSC	1005	15	10 Jun ± 2.2	12 Jun ± 2.2	15 Jun ± 2.3	18 Jun ± 2.4	22 Jun ± 2.3	27 Jun ± 2.2	29 Jun ± 2.2	15 ± 2.4	8 ± 1.9

* Variance (standard deviation) accounted for by the random effect of site-year was 31.90 (5.65) for 10% Date, 39.08 (6.25) for 50% Date, 33.41 (5.78) for 90% Date, and 22.69 (4.76) for Span.

[†] AGWT, American green-winged teal; AMWI, American wigeon; BWTE, blue-winged teal; GADW, gadwall; LESC, lesser scaup; MALL, mallard; NOPI, northern pintail; NSHO, northern shoveler; WWSC, white-winged scoter

Table A.2 Model selection tables for Span (10–90% Dates) and End (90% Date) of Nesting by prairie ducks. Sample sizes (nests and site-years) are given in Table A.1.

Response Variable	Model Structure*	$K^{\dagger}$	Log likelihood	$AIC_c^{\ddagger}$	$\Delta AIC_c^{\S}$	$\omega_i^{\|}$
Span of Nesting	Species * Spring Pond	18	-2760.48	5557.9	0	0.56
	Species * Spring Pond + Latitude + Longitude	20	-2758.70	5558.5	0.65	0.40
	Species + Spring Pond	11	-2771.15	5564.6	6.77	0.02
	Species + Spring Pond + Latitude + Longitude	13	-2769.38	5565.2	7.36	0.01
End of Nesting	Species * Spring Pond + Latitude + Longitude	20	-2638.33	5317.8	0	0.69
	Species * Spring Pond	18	-2641.25	5319.4	1.63	0.31
	Species + Spring Pond + Latitude + Longitude	13	-2651.16	5328.8	11.02	0
	Species + Spring Pond	11	-2654.00	5330.4	12.57	0

* The same site-year random effects structure was used in all models; models with interaction terms (e.g., Species * Spring Pond) also incorporate main effects.

† Number of parameters included in the model.

‡ Akaike's information criterion corrected for small sample size (AIC_c).

§ Difference in AIC_c (ΔAIC_c) values between each model and the model with the lowest AIC_c are given.

‖ The Akaike weight (ω_i) or likelihood of a model given the set of models.

Table A.3 Parameter estimates ± SE from the best-approximating model relating Span and End of nesting to species, site-specific pond counts, latitude, and longitude. AGWT represents the intercept. Model structure is given in Table A.2 [a]. Species acronyms are given in Table A.1.

Response Variable		Parameter Estimates			
		Species	Spring Pond	Latitude	Longitude
Span of Nesting	Intercept (AGWT)	31.39 ± 1.52***	-0.97 ± 1.50[b]		
	AMWI	-7.78 ± 1.95***	3.64 ± 1.99*		
	BWTE	-1.84 ± 1.60	2.55 ± 1.58†		
	GADW	-9.43 ± 1.64***	2.58 ± 1.58†		
	LESC	-12.04 ± 2.01***	1.75 ± 1.98		
	MALL	8.69 ± 1.62***	1.58 ± 1.59		
	NOPI	8.73 ± 1.75***	1.83 ± 1.73		
	NSHO	-2.16 ± 1.63	3.21 ± 1.61**		
End of Nesting	Intercept (AGWT)	161.43 ± 19.35***	-1.59 ± 1.25[b]	0.84 ± 0.40**	0.36 ± 0.13***
	AMWI	0.36 ± 1.56	3.78 ± 1.59**		
	BWTE	1.77 ± 1.29	1.73 ± 1.27		
	GADW	4.21 ± 1.32***	2.14 ± 1.29*		
	LESC	8.67 ± 1.60***	2.49 ± 1.57†		
	MALL	-1.24 ± 1.30	3.49 ± 1.28***		
	NOPI	-6.81 ± 1.41***	1.19 ± 1.39		
	NSHO	-2.44 ± 1.31**	2.54 ± 1.29**		

[a] Variance (standard deviation) accounted for by the random effect of site-year in each of the best-approximating models was 21.89 (4.68) for Span of nesting (10–90% Dates), and 32.71 (5.72) for End of nesting (90% Date).

[b] The first β corresponds to the main effect of spring pond count on the nesting variable; the other βs in the column refer to interaction effects between species and pond count.

†$p < 0.15$, * $p < 0.10$, ** $p < 0.05$, *** $p < 0.01$

A.6 FIGURES

Figure A.1 Least squares mean estimates of Span of nesting (number of days) and End of nesting (date 160 is ~June 9) in relation to Start of nesting (date 120 is ~Apr 30) and corresponding 95% confidence intervals for each species. Sample sizes in Table A.1. Estimates were derived from a mixed effects model with site-year as a random effect and species as a fixed effect. Species acronyms are: AGWT, American green-winged teal; AMWI, American wigeon; BWTE, blue-winged teal; GADW, gadwall; LESC, lesser scaup; MALL, mallard; NOPI, northern pintail; NSHO, northern shoveler; WWSC, white-winged scoter.

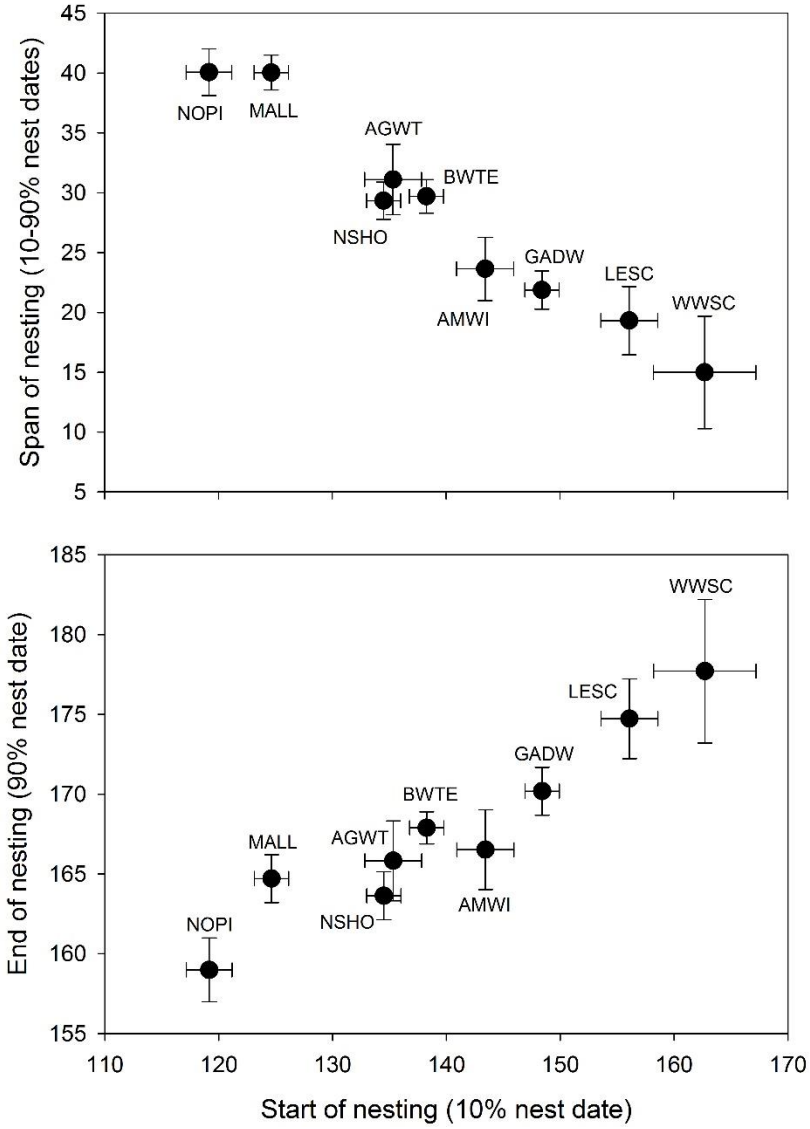
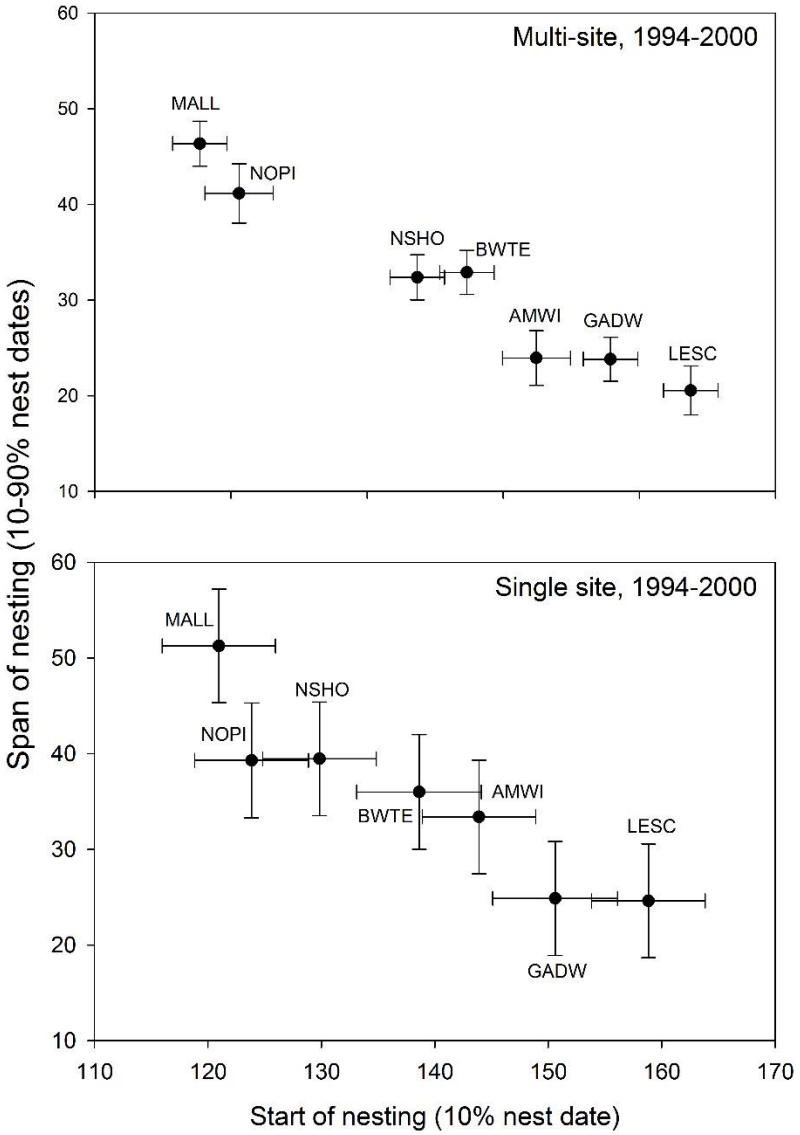


Figure A.2 Least squares mean estimates of Span of nesting (number of days) versus Start of nesting (date 120 is ~Apr 30) and corresponding 95% confidence intervals for each species in each respective study from 1994-2000 , DUC sites (multi-site) and SDNWA (single site) combined. AGWT has been omitted due to low sample size at SDNWA; sample sizes are given in Supplementary Material A.1. Estimates were derived from a mixed effects model with random year (SDNWA) or site-year (DUC) effects and fixed effects of species. Species acronyms are listed in Fig. A.1 caption.



A.7 SUPPLEMENTARY MATERIAL

Supplementary Material A.1 Number of nests, number of site-years or years, and least squares mean (LSmean; calendar date) parameter estimates ± SE of Start (10% nest date), Span (number of days difference between 10–90% nest dates), and End (90% date) of nesting for each species in respective studies, 1994-2000. Estimates were derived from a mixed effects model with random site-year (DUC, multiple sites and years)† or year (SDNWA, single site)* effects and fixed effects of species. Species acronyms are given in Table A.1.

	DUC					SDNWA				
Species	*N*	Site-Years	Start	Span	End	*N*	Years	Start	Span	End
AGWT	368	23	13 May ± 1.1	35 ± 1.2	17 Jun ± 1.3	19	2	21 May ± 3.9	33 ± 5.5	2 Jun ± 3.9
AMWI	291	16	22 May ± 1.2	24 ± 1.4	15 Jun ± 1.5	149	7	24 May ± 2.5	33 ± 3.0	26 Jun ± 2.2
BWTE	4264	25	17 May ± 1.0	33 ± 1.2	19 Jun ± 1.2	505	7	19 May ± 2.5	36 ± 3.0	24 Jun ± 2.2
GADW	1917	25	28 May± 1.0	24 ± 1.2	21 Jun ± 1.2	509	7	31 May ± 2.5	25 ± 3.0	24 Jun ± 2.2
LESC	329	20	3 Jun ± 1.1	21 ± 1.3	23 Jun ± 1.3	139	7	8 Jun ± 2.5	25 ± 3.0	2 Jul ± 2.2
MALL	3945	25	28 Apr ± 1.0	46 ± 1.2	13 Jun ± 1.2	946	7	1 May ± 2.5	51 ± 3.0	21 Jun ± 2.2
NOPI	374	13	1 May ± 1.3	41 ± 1.6	11 Jun ± 1.6	91	7	4 May ± 2.5	39 ± 3.0	12 Jun ± 2.2
NSHO	1813	24	14 May ± 1.1	32 ± 1.2	15 Jun ± 1.2	244	7	10 May ± 2.5	39 ± 3.0	18 Jun ± 2.2

† Variance (standard deviation) for the random effect of site-year was 13.14 (3.63) for Start, 7.94 (2.82) for Span, and 12.75 (3.57) for End of nesting.

* Variance (standard deviation) for the random effect of year was 20.40 (4.52) for Start, 0.64 (0.80) for Span, and 9.67 (3.11) for End of nesting.

APPENDIX B. COMPLETE RESULTS FROM POPULATION ESTIMATION ANALYSES PRESENTED IN CHAPTER 2

Table B.1 Model selection tables for population estimates (log-scaled; $\ln(N_{t+1})$) related to the previous year's estimate ($\ln(N_t)$), current year's pond count (log-scaled; $\ln(POND_{t+1})$), and regional differences (REGION) for each species. All models that include and interaction term also include the main effects of the variable within the interaction.

Model Structure	K[†]	Log likelihood	AIC_c[‡]	ΔAIC_c[§]	ω_i[‖]
American green-winged teal					
$\ln(N_t) + \ln(POND_{t+1}) + REGION$	5	-31.46	73.7	0	0.73
$\ln(N_t) + \ln(POND_{t+1}) * REGION$	6	-31.44	76.0	2.3	0.23
$\ln(N_t) + \ln(POND_{t+1})$	4	-35.40	79.3	5.59	0.04
American wigeon					
$\ln(N_t) + \ln(POND_{t+1}) * REGION$	6	-14.71	42.6	0	0.48
$\ln(N_t) + \ln(POND_{t+1}) + REGION$	5	-15.94	42.7	0.11	0.46
$\ln(N_t) + \ln(POND_{t+1})$	4	-19.03	46.6	4.01	0.07
Blue-winged teal					
$\ln(N_t) + \ln(POND_{t+1}) * REGION$	6	-4.44	22.0	0	0.58
$\ln(N_t) + \ln(POND_{t+1}) + REGION$	5	-5.93	22.7	0.63	0.42
$\ln(N_t) + \ln(POND_{t+1})$	4	-18.78	46.1	24.07	0
Canvasback					
$\ln(N_t) + \ln(POND_{t+1}) * REGION$	6	-13.97	41.1	0	0.56
$\ln(N_t) + \ln(POND_{t+1}) + REGION$	5	-15.38	41.6	0.47	0.44
$\ln(N_t) + \ln(POND_{t+1})$	4	-25.09	58.7	17.62	0
Gadwall					
$\ln(N_t) + \ln(POND_{t+1}) + REGION$	5	-5.50	21.8	0	0.67
$\ln(N_t) + \ln(POND_{t+1}) * REGION$	6	-5.26	23.7	1.85	0.27
$\ln(N_t) + \ln(POND_{t+1})$	4	-9.07	26.7	4.85	0.06
Lesser scaup					
Mallard					
$\ln(N_t) + \ln(POND_{t+1}) * REGION$	6	28.37	-43.6	0	0.86
$\ln(N_t) + \ln(POND_{t+1}) + REGION$	5	25.14	-39.5	4.12	0.11
$\ln(N_t) + \ln(POND_{t+1})$	4	22.60	-36.7	6.92	0.03
Northern pintail					
$\ln(N_t) + \ln(POND_{t+1}) + REGION$	5	-31.93	74.7	0	0.69
$\ln(N_t) + \ln(POND_{t+1}) * REGION$	6	-31.84	76.8	2.15	0.24
$\ln(N_t) + \ln(POND_{t+1})$	4	-35.24	79.0	4.34	0.08
Northern shoveler					
$\ln(N_t) + \ln(POND_{t+1}) + REGION$	5	-11.53	33.9	0	0.62
$\ln(N_t) + \ln(POND_{t+1}) * REGION$	6	-10.90	34.9	1.08	0.36
$\ln(N_t) + \ln(POND_{t+1})$	4	-15.84	40.2	6.34	0.03
Redhead					
$\ln(N_t) + \ln(POND_{t+1}) * REGION$	6	-24	61.3	0	0.80
$\ln(N_t) + \ln(POND_{t+1})$	4	-28.14	64.8	3.56	0.14
$\ln(N_t) + \ln(POND_{t+1}) + REGION$	5	-27.81	66.4	5.16	0.06
Ruddy duck					
$\ln(N_t) + \ln(POND_{t+1})$	4	-52.15	112.8	0	0.67
$\ln(N_t) + \ln(POND_{t+1}) + REGION$	5	-52.13	115.1	2.24	0.22
$\ln(N_t) + \ln(POND_{t+1}) * REGION$	6	-51.64	116.4	3.59	0.11

$\ln(N_t) + \ln(POND_{t+1}) + REGION$	5	-18.71	48.2	0	0.72
$\ln(N_t) + \ln(POND_{t+1}) * REGION$	6	-18.63	50.4	2.18	0.24
$\ln(N_t) + \ln(POND_{t+1})$	4	-22.81	54.1	5.92	0.04

† Number of parameters included in the model.

‡ Akaike's information criterion corrected for small sample size (AIC_c).

§ Difference in AIC_c (ΔAIC_c) values between each model and the model with the lowest AIC_c are given.

ǁ The Akaike weight (ω_i) or likelihood of a model given the set of model.

APPENDIX C. COMPLETE RESULTS FROM TIMING OF NESTING AND NEST SURVIVAL ANALYSES FOR LESS COMMON SPECIES PRESENTED IN CHAPTER 3

Table C.1 Model selection tables including parameter estimates ± SE for all models in the candidate set for **timing of nesting** related to moisture anomaly index (MAI), Winter ENSO (WINT_ENSO), and spring temperature (SPR_T; residuals, SPR_T_{resid}) for each of the less common species. Models that contain interactions also include the main effects of the variables within those interactions. Sample sizes (nests and site-years) for each species are given in Table 3.1.

	Parameter Estimates ± SE								
Model Structure*	MAI	WINT_ENSO	SPR_T/SPR_Tresid	WINT_ENSO * SPR_Tresid	K†	Log likelihood	AIC_c‡	ΔAIC_c§	ω_i‖
American green-winged teal									
MAI + SPR_T	-0.88 ± 3.13		-0.97 ± 0.75		6	-375.77	764.3	0	0.22
MAI + WINT_ENSO + SPR_T_{resid}	-0.90 ± 3.16	0.05 ± 0.78	-1.06 ± 0.77		7	-374.98	765.0	0.68	0.16
MAI	-0.06 ± 3.07				5	-377.23	765.0	0.71	0.16
WINT_ENSO + SPR_T_{resid} + WINT_ENSO * SPR_T_{resid}		-0.16 ± 0.81	-1.54 ±0.95	-1.34 ± 1.52	7	-375.36	765.7	1.44	0.11
MAI + WINT_ENSO	-0.04 ± 3.12	0.16 ± 0.79			6	-376.54	765.8	1.55	0.10
SPR_T (Biological null)			-0.94 ± 0.72		5	-377.86	766.3	1.97	0.08
intercept only (Statistical null)					4	-379.27	766.9	2.6	0.06
WINT_ENSO + SPR_T_{resid}		0.07 ± 0.77	-1.01 ± 0.74		6	-377.08	766.9	2.63	0.06
WINT_ENSO		0.16 ± 0.77			5	-378.59	767.7	3.42	0.04
American wigeon									
WINT_ENSO + SPR_T_{resid} + WINT_ENSO * SPR_T_{resid}		-0.90 ± 0.82	-2.42 ± 1.05	-3.21 ± 1.58	7	-335.65	686.4	0	0.35
MAI + SPR_T	-2.61 ± 3.73		-1.75 ± 1.04		6	-337.19	687.2	0.79	0.23
MAI + WINT_ENSO + SPR_T_{resid}	-2.58 ± 3.82	-0.60 ± 0.90	-1.76 ± 1.07		7	-336.41	687.9	1.51	0.16
MAI	-1.09 ± 3.68				5	-339.56	689.7	3.29	0.07
SPR_T (Biological null)			-1.58 ± 1.00		5	-339.67	689.9	3.50	0.06
MAI + WINT_ENSO	-1.11 ± 3.77	-0.25 ± 0.89			6	-338.74	690.3	3.88	0.05
WINT_ENSO + SPR_T_{resid}		-0.54 ± 0.89	-1.59 ± 1.03		6	-338.89	690.6	4.19	0.04

intercept only (Statistical null)					4	-341.82	692.0	5.61	0.02
WINT_ENSO		-0.25 ± 0.87			5	-341.02	692.6	6.19	0.02
Lesser scaup									
MAI + WINT_ENSO + SPR_T_{resid}	3.08 ± 3.84	0.82 ± 1.08	0.41 ± 1.47		7	-322.61	660.4	0	0.21
MAI + SPR_T	2.81 ± 3.77		0.63 ± 1.41		6	-323.82	660.5	0.12	0.20
MAI + WINT_ENSO	2.97 ± 3.74	0.77 ± 1.04			6	-323.95	660.7	0.38	0.17
MAI	2.60 ± 3.68				5	-325.18	660.9	0.59	0.16
WINT_ENSO + SPR_T_{resid} + WINT_ENSO * SPR_T_{resid}		0.59 ± 1.11	0.11 ± 1.56	-0.81 ± 2.10	7	-323.47	662.1	1.71	0.09
WINT_ENSO + SPR_T_{resid}		0.69 ± 1.06	0.30 ± 1.45		6	-325.2	663.2	2.88	0.05
SPR_T (Biological null)			0.50 ± 1.39		5	-326.34	663.3	2.92	0.05
WINT_ENSO		0.65 ± 1.03			5	-326.50	663.6	3.24	0.04
intercept only (Statistical null)					4	-327.64	663.7	3.32	0.04

* The same site-year and habitat random effects structure was used in all models.

† Number of parameters included in the model.

‡ Akaike's information criterion corrected for small sample size (AIC_c).

§ Difference in AIC_c (ΔAIC_c) values between each model and the model with the lowest AIC_c are given.

ǁ The Akaike weight (ω_i) or likelihood of a model given the set of model.

Table C.2 Model selection tables including parameter estimates ± SE for all models for **daily nest survival** related to moisture anomaly index (MAI), Winter ENSO (WINT_ENSO), and spring temperature (SPR_T; residuals, SPR_T_{resid}) for each of the three less common species. Over-dispersion parameter (ĉ) is reported for each species. Models below the dashed line for any given species did not converge. Sample sizes (nests and site-years) for each species are given in Table 3.1.

	Parameter Estimates ± SE								
Model Structure*	RCID	$RCID^2$	MAI	WINT_ENSO	SPR_T/SPR_T_{resid}	K†	$QAIC_c$‡	$\Delta QAIC_c$§	ω_i‖
American green-winged teal **(ĉ=2.06)**									
RCID + RCID2	-0.514 ± 1.011	2.910 ± 1.272				4	437.2	0.00	0.27
RCID	1.724 ± 0.296					3	437.8	0.61	0.20
RCID + RCID2 + WINT_ENSO	-0.558 ± 1.012	2.988 ± 1.274		-0.152 ± 0.108		5	438.4	1.14	0.15
RCID + RCID2 + MAI	-0.536 ± 1.013	2.930 ± 1.272	0.171 ± 0.440			5	439.2	1.99	0.10
RCID + RCID2 + SPR_T	-0.505 ± 1.012	2.905 ± 1.272			0.020 ± 0.107	5	439.3	2.04	0.10
RCID + RCID2 + WINT_ENSO + SPR_Tresid	-0.539 ± 1.012	2.980 ± 1.273		-0.148 ± 0.108	0.047 ± 0.105	6	440.3	3.11	0.06
RCID + RCID2 + WINT_ENSO + MAI	-0.582 ± 1.013	3.010 ± 1.275	0.174 ± 0.423	-0.152 ± 0.107		6	440.3	3.13	0.06
RCID + RCID2 + SPR_T + MAI	-0.527 ± 1.013	2.926 ± 1.272	0.200 ± 0.452		0.030 ± 0.109	6	441.2	4.02	0.04
RCID + RCID2 + WINT_ENSO + SPR_Tresid + MAI	-0.566 ± 1.012	3.006 ± 1.273	0.231 ± 0.433	-0.146 ± 0.107	0.060 ± 0.107	7	442.3	5.05	0.02
intercept only						2	453.9	16.64	0.00
American wigeon **(ĉ=2.01)**									
RCID + RCID2	1.918 ± 1.062	-2.562 ± 1.236				4	386.1	0.00	0.32
RCID + RCID2 + SPR_T	2.067 ± 1.061	-2.781 ± 1.239			0.251 ± 0.168	5	387.1	0.99	0.20
RCID + RCID2 + MAI	1.977 ± 1.064	-2.634 ± 1.239	-0.427 ± 0.617			5	387.9	1.83	0.13
RCID + RCID2 + WINT_ENSO	1.894 ± 1.061	-2.523 ± 1.236		0.100 ± 0.144		5	387.9	1.83	0.13
RCID + RCID2 + WINT_ENSO + SPR_Tresid	2.044 ± 1.062	-2.744 ± 1.241		0.143 ± 0.143	0.238 ± 0.169	6	389.0	2.94	0.07
RCID + RCID2 + SPR_T + MAI	2.092 ± 1.063	-2.809 ± 1.242	-0.229 ± 0.613		0.236 ± 0.173	6	389.1	3.00	0.07
RCID + RCID2 + WINT_ENSO + MAI	1.952 ± 1.063	-2.594 ± 1.239	-0.404 ± 0.611	0.094 ± 0.143		6	389.8	3.70	0.05
RCID + RCID2 + WINT_ENSO + SPR_Tresid + MAI	2.068 ± 1.063	-2.772 ± 1.243	-0.219 ± 0.610	0.137 ± 0.144	0.224 ± 0.173	7	391.0	4.96	0.03
intercept only									

RCID									
***Lesser scaup* (ĉ=2.04)**									
RCID	-1.042 ± 0.425					3	375.3	0.00	0.32
intercept only						2	376.2	0.91	0.20
RCID + RCID2	-1.704 ± 1.306	0.884 ± 1.643				4	377.2	1.92	0.12
RCID +SPR_T	-1.048 ± 0.425				-0.097 ± 0.229	4	377.3	1.97	0.12
RCID +WINT_ENSO + MAI	-1.026 ± 0.426		0.975 ± 0.648	-0.182 ± 0.169		5	377.5	2.17	0.11
RCID + SPR_T + MAI	-1.001 ± 0.426		1.080 ± 0.666		-0.045 ± 0.224	5	378.0	2.71	0.08
RCID + WINT_ENSO +SPR_Tresid	-1.072 ± 0.424			-0.226 ± 0.173	-0.025 ± 0.228	5	378.6	3.31	0.06
RCID + MAI									
RCID + WINT_ENSO									
RCID + WINT_ENSO +SPR_Tresid + MAI									

* The same site-year and habitat random effects structure was used in all models.

† Number of parameters included in the model.

‡ Akaike's Information Criterion corrected for sample size and over-dispersion ($QAIC_c$).

§ Difference in $QAIC_c$ ($\Delta QAIC_c$) values between each model and the model with the lowest $QAIC_c$ are given.

ǁ The Akaike weight (ω_i) or likelihood of a model, given the set of models.